Have the Genetic Patterns of Fishes been Altered by Introductions or by Selective Fishing?[1,2]

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ABSTRACT

This paper is a review of some of the literature dealing with changes in freshwater fish populations following exploitation or after introduction of exotic species. The object of the review was to look for changes that could be attributed to alterations in the gene pools of the affected populations. Very little concrete evidence could be found, either because the investigations reviewed were not looking for genetic changes, or because such changes did not occur. Changes in some salmonids may be assigned to introgressive hybridization, particularly where rainbow and cutthroat trout have been put together on the Eastern Slopes. In many cases, however, exotics have apparently failed to contribute to the gene pool of the resident population, and most hybrids, when they occur, have been of low fertility.

Fishes have a remarkable ability to respond to changes in population density by altered growth rates and times of maturity. These changed characters are not necessarily due to genetic changes and may be explained by assuming that fishes are pre-adapted to a wide range of conditions. There is a rather speculative suggestion that angling may select less intelligent fish, leading to an upgrading in intelligence of the fish. The general conclusion is that in the light of the existing evidence, great caution must be used in attributing to man-induced changes in fish populations changes in the genetic pattern.

INTRODUCTION

The original version of this paper was presented at a symposium on speciation of aquatic organisms sponsored by the Canadian Committee on Freshwater Fisheries Research. There was a feeling that the thinking of fishery biologists was coloured, to some extent, by assumptions that certain fishery practices had an effect on the genetic pattern in fishes. An example is the assumption that gill-nets, by selecting the larger and, hence, faster growing fishes would exert a selection against the genotype for rapid growth. Another is the theory that differential exploitation might stimulate the less exploited species to evolve in such a way as to fill the niches formerly occupied by the favoured species. Still other examples exist in the possible effects of the introduction of exotic species; such exotics could themselves prove more successful, or hybrids, or new genetic patterns produced by hybridization (introgression), might come to outnumber the original species. A review of the literature which might establish or disprove such assumptions seemed in order.

Such a review could be performed by a geneticist or by an aquatic biologist; either would find himself in unfamiliar territory. The author, an aquatic biologist, makes no pretense of complete familiarity with current genetical thinking and research.

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The review is divided into two parts: I. Effects of Introduction of Exotics and, II. Effects of Selection by Fishing.

I. EFFECTS OF INTRODUCTION OF EXOTICS

There are several ways in which exotic fishes might alter the genetic structure of the population into which they are introduced. These are: (1) by hybridization; (2) through becoming more successful than native species and displacing them; and (3), by themselves responding to the new conditions and evolving into "new" fishes.

(1) HYBRIDIZATION. In fish populations the introduction of exotic species favours hybridization. Where hybrids have been found in nature it is generally in a situation where a small population of one species is mixed with a large population of another, related species (Hubbs, Walker and Johnson, 1943). A considerable number of hybrids which have arisen in this way have been reported. In general these fishes appear to be sterile and the genetic pattern of the breeding population remains unchanged. An interesting exception has been described by Hubbs (1955); a hybrid between a native and an introduced chub eventually, with its exotic parent, came to outnumber the native species.

More pertinent, perhaps, are the numerous salmonid hybrids which have been deliberately created by fish culturists. Rainbow and cutthroat trout have been both deliberately and unintentionally crossed in many western hatcheries. Stenton (1950) reports high viability for the splake, a cross of the lake trout and the eastern brook trout. Buss and Wright (1956) crossed the common species of trout and char (except cutthroat and Dolly Varden). All the crosses, except some of the reciprocals, produced some hybrids, but the precentage of surviving hybrid fry was low. The lake trout by brook trout cross was most successful, but less so than in Stenton's experiments. The char hybrids proved fertile in backcrosses; the trout hybrids were not. The marked reduction in fertility of all the salmonid hybrids ensures their failure under natural conditions.

While the hybrids may be extremely "fit" in the Darwinian sense, if they produce much smaller numbers of progeny than their parental species, they cannot compete beyond the first few generation. Wright (1940) and other geneticists have pointed out that a reduction of only 0.1 per cent in viability will override the highest observed favourable mutation rates.

There is, as yet, no evidence of the occurrence of allotetraploids in fishes which could lead to new and viable species.

As well as simple hybridization, there is the possibility of introgressive hybridization, a more subtle and, probably, more effective means of altering the gene pool of a population. Even where hybrids are normally sterile, out of many individuals a small percentage usually produce some viable gametes (e.g. in mules). On backcrossing with the parent species, such hybrids will introduce new genes to the parental gene pool. There is some evidence that introgression has occurred in salmonids. In the South Saskatchewan drainage in Alberta the commonest trout in the larger rivers is a "rainbow" which clearly has a number of cutthroat characteristics, notably, a loss of the migratory habit (Gilmour, 1950.) The cutthroat

was the native fish and rainbow were introduced. In the smaller streams the native cutthroat is still much more numerous but it is almost impossible to find a population which does not show some rainbow "blood". This mutual "contamination" among salmonids is possibly fairly general. Personal correspondence with taxonomists such as Dr. R. R. Miller indicates that it is difficult to find cutthroat and rainbow stocks which are definitely "pure". On the other hand, as Smith and Needham (1942) have pointed out, there is a general failure of exotics to survive long enough to contribute to the gene pool; an analogous situation is the poor survival of hatchery stocks superimposed on residents of the same species (Miller, 1955 and many other authors). Perhaps cutthroat-rainbow introgression represents a special case as, on the Eastern Slopes of the Rocky Mountains, they may well be sibling species of relatively recent origin (personal opinion).

(2) DISPLACEMENT OF NATIVE SPECIES BY EXOTICS. Hubb's example of an introduced chub becoming more successful than the native species has already been cited. This is the only well-authenticated example of displacement that this reviewer could find. Among the salmonids there seems to be some evidence of displacement, although it is not clear that the observed changes might not be due to introgression. According to Miller and Alcorn (1954) the native trout is disappearing in Nevada. As already mentioned, the native cutthroat trout is becoming rare in South Saskatchewan waters in Alberta, due either to displacement by rainbow or (more likely) displacement by a "race" resulting from introgression. In this connection it is remarkable to note the apparently peaceful coexistence of these two species in streams on the Western Slopes.

(3) CHANGE IN INTRODUCED STOCK INDUCED BY ISOLATION FROM ORIGINAL POPULATION. An exotic species, established in a new environment, would presumably be immediately exposed to a new set of selection pressures, and evolutionary changes could be anticipated. Nevertheless, there is little or no evidence that genetic change has occurred. This may be due to the short times involved, or it may be because of the remarkable plasticity of fishes, such that they are pre-adapted to a very wide range of environmental conditions. On the other hand, the absence of evidence may be simply because no one has looked for it. However, there is a great deal of evidence that no easily observable changes have occurred in many species of fishes introduced to new environments. To quote but a few examples: the Kamloops trout in the Cowichan River (Neave, 1949); smallmouth black bass on Vancouver Island; tench in United States; brown trout all over North America; rainbow trout in New Zealand; carp in the Great Lakes and elsewhere; eastern brook trout in Western North America; sea-run brown trout on the Atlantic Coast.

The general failure of major morphological distinctions to appear in these displaced species, is perhaps, not unexpected in view of the numerous "races" of fishes which are separated on other than morphological grounds. These incipient species have not yet evolved to the point where they may be distinguished from parent groups by morphological characters. Examples are provided by the races of Pacific salmon, the chars in the Karluk drainage, Alaska (Delacy and Morton, 1943); the races of sturgeon in the Caspian Sea (Gerbilskii, 1955); lake chars

in Europe (Huxley, 1942); Moser River sea-run and non sea-run trout (Wilder, 1952). It is worth pointing out that some of these races are not proven to be genetically distinct. Thus White and Huntsman (1938) found no evidence that spring and fall races of Atlantic salmon differ. When the fry of early-running races were transplanted to a stream normally occupied by fall races, they grew up with behavioral characteristics more like the usual inhabitants of the stream, i.e., the fall race.

II. EFFECTS OF SELECTION BY FISHING

Selection by fishing could exert effects on the genetic pattern in the following ways: (1) differential removal of faster growing fish, with resulting selection for slow growth; (2) heavy exploitation causing the division of a panmictic group into allopatric groups or demes, thus allowing for the fixation of new, possibly non-adaptive, gene combinations in these small groups; interbreeding between neighbouring demes then permits the new combinations (or, perhaps, new, non-adaptive mutations) to spread throughout the population (Sewall Wright effect); (3) differential exploitation of species leading to adaptive radiation in the less exploited species; (4) differential removal, by angling, of the less intelligent fish, thus selecting for intelligence. This could also be selection for timidity, or selection against psychic dominants.

(1) DIFFERENTIAL REMOVAL OF FASTER GROWING FISH WITH SELECTION FOR SLOW GROWTH. Working with a small brood stock, under controlled conditions, it is easy to alter the genetic pattern of salmonids. Millenbach (1950) selected from rainbow brood stock for 2-year-old spawners. He was able to change the stock rapidly; in one experiment the percentage of 2-year-spawners rose from 4.7 to 84.3 in three generations. Lewis (1949) successfully selected for increased growth rate, fecundity and viability of eggs in stocks of fall-spawning rainbow trout. Schaeperclaus (1933) states that carp have been successfully selected for rapid growth in ponds.

These examples of selection are from brood stocks, maintained, like livestock, under artificial conditions. The gene-complexes selected could easily have pleiotropic or linkage effects which would be selected against in nature. Millenbach's early maturing stock, for example, proved to be slow growing and lacking in fecundity.

Neave and Pritchard (1947) performed a selection for early maturing under natural conditions, that is, using wild fish. They used early-maturing coho salmon males (Jacks) to fertilize eggs; the resulting adults showed only the usual proportion of early maturing males. This experiment lasted for only one generation so no very large change could be expected.

It is reasonable to postulate that the faster growing members of a fish population do not owe their rapid growth entirely to genetic factors, but that due to some accident of early life, got some advantage over their fellows which allowed them to better realize the growth potential possessed by all the population. It is well known that certain year classes grow faster than others (e.g., Svärdson, 1953). These can be attributed to reduced competition.

The author knows of no instances of changed growth rates in populations where it is not reasonable to attribute the results entirely to environmental effects such as reduced competition, or increased food supply. Of course, it cannot be denied that some of the observed changes may be attributable to genetic change.

(2) HEAVY EXPLOITATION CAUSING THE DIVISION OF A PANMICTIC GROUP INTO ALLOPATRIC GROUPS OR DEMES, THUS LEADING TO THE SEWALL WRIGHT EFFECT. In commercial fisheries in large lakes we may have a duplication of Wright's model (Wright, 1940, 1943, 1950). Heavy fishing could create separate groups, with some interchange of breeding individuals between groups. This allows fixation of random mutations or new gene combinations in the small groups and then their spread throughout the population. For this scheme to be effective the breeding population should number 100,000 to 1 million and the demes, 1,000 to 10,000, figures which would fit a number of commercial fisheries. The numerous studies of commercial fisheries have not looked for genetic change attributable to this effect. However, Ricker (1950) pointed out that races of Pacific salmon are not attributable to exploitation; in fact the races have arisen from causes other than cyclic abundance and fishing. As Royal (1953) has stated, the recovery of early-run, depleted races has been due to protecting them from further exploitation and not to filling in from plentiful later-run races.

There is a great deal of evidence from natural disasters that reducing a fish population does not necessarily lead to genetic change. One might expect fish to react like the moths studied by Ford and Ford (1930); these authors showed that a population succeeding a very small population was recognizably different. Fish, and perhaps mammals also, fail to show change following a population crash. Hares, for example, recover from periodic scarcities with no visible alteration. Yet it is well established that isolated small populations of fishes do undergo extensive genetic change *in new environments*. Worthington (1940) describes such speciation in African lakes where there is absence of predation and isolation from neighbouring watersheds. He also points out that in glacial lakes that have drainage systems, changing ecological conditions have not produced speciation but merely emigration and immigration. The basic situation leading to change would seem to be presence of *new environmental conditions* with no opportunity to move away. It is perhaps not surprising, then, that fish recover from periods of scarcity without visible genetic change when they remain in the same environment. There are numerous published instances. To mention but a few: Beckman (1943) observed a great increase in rock bass following a reduction in population density. The same author (1950) observed populations of fish recovering from winter-kills in four Michigan Lakes. Svärdson (1949) refers to the same phenomenon in Swedish lakes. All across the Canadian prairies frequent winter-kills have almost eliminated perch and pike populations repeatedly, but the new populations are still unaltered pike and perch. The recovery of halibut on the Pacific Coast has not been attended by any *observed* genetic change. Saugers and doré in Lake Manitoba, have recovered from a period of very small populations (Kennedy, 1948).

(3) DIFFERENTIAL EXPLOITATION OF SPECIES. As Worthington (op. cit.) has shown, a species in a new environment may undergo extensive speciation. It seems to follow logically, that where several species occupy all the niches in a given environment, if one or more species are removed, the remaining species would spread into the vacated niches, altering genetically as they became adapted to them. If this is a valid argument, it is reasonable to suppose that in a commercial fishery that uses some species and not others, the non- or less exploited species would undergo some adaptive radiation and spread into the niches whose inhabitants were being exploited. A good example of where this might be expected is provided by the whitefish populations of some of the Swedish lakes. Svärdson (1953) has described several of these lakes which contain three or four sibling and sympatric whitefish species. Some of the species are exploited because of greater size and vulnerability whereas others are not. The presence of one species, in one lake, was not known to the fishermen. In spite of this differential exploitation in some lakes, Svärdson has been unable to detect any differences between the unused species in the fished lakes and the same species in the unfished lakes. Parallels of this situation undoubtedly occur in the Great Lakes.

Except for Svärdson's work, studies of the changes in population in lakes subjected to fishing have not looked specifically for evidence of genetic change. Ascendancy of unexploited stocks has occurred, e.g., in Lake of the Woods (Carlander, 1949). But in most lakes not even the increase of non-exploited species has been noted. Examples have been published by Smith and Krefting (1954) in Red Lakes, Minnesota over a 24-year period; by Murphy (1951) in Clear Lake; and by Thompson and Hutson (1951) in Lake Pawhuska.

The small, non-sea-run sockeye salmon known as the Kokanee provides an interesting puzzle. It evidently arose from the anadromous sockeye, but it has not been demonstrated how this came about. Kokanee occur in lakes with access to the sea; often, indeed, sea-run sockeye visit the same lakes to spawn. Ricker (1940) postulated that exploitation of the sea-run salmon may have helped establish predominant Kokanee populations in some of the head water lakes. Foerster (1947) showed that Kokanee could be the parents of salmon that ran to sea and returned indistinguishable from normal anadromous sockeye. Thus it is an open question as to what part exploitation may or may not have played in the evolution of the Kokanee.

(4) DIFFERENTIAL REMOVAL BY ANGLING OF THE LESS INTELLIGENT FISH, THUS SELECTING FOR INTELLIGENCE. A number of authors have noted pronounced interspecific differences in catchability of fish by angling. Manges (1951) showed that crappies, fished for more heavily than bass, were caught at a lower rate. The greater difficulty of catching brown trout as compared to brook and rainbow has been commented on by numerous authors. Schuck (1942) showed that brook trout were harvested in proportion to their numbers, but that brown trout were not. Thorpe, Rayner and Webster (1947) showed that in a part of the Blackledge River, anglers removed brook trout first, then rainbow, then browns. Catches were proportional to numbers except in some of the brown trout plants. Neave (1949) noted that brown trout in Cowichan River were not taken in proportion

to their abundance. Cooper (1952) showed that brook trout in his investigations were 7½ times more vulnerable to angling than brown trout. This greater resistance to angling by brown trout is possibly a result of superior intelligence. Recently Adelman and Bingham (1956) subjected trout to learning and discrimination tests. Brown trout learned size discrimination faster than brook or rainbow in the first test; brown and rainbow were faster than brook trout in the second test. Brown trout have been subjected to angling for several thousand years; brook and rainbow only two hundred years. Possibly this is an example of genetic change—angling has selected a gene complex that produces a more intelligent, probably, also, more wary trout.

It seems probable that this sort of selection is going on continuously. There is evidence that vulnerability to lures is a genetic variable amongst individuals of trout populations. It is well known and bitterly lamented that angling for wild fish grows progressively less successful, not only within a season, but over a period of years. It is not unreasonable to assume that the les wary or more unintelligent fish are soon removed, providing a strong selection for wariness and/or intelligence. This is at least a better assumption than the anglers', i.e., that the populations have been seriously depleted; this explanation has frequently been disproven.

A complication in this theory of selecting for intelligence is the possiblity of selecting for timidity; the more vulnerable fish may be the psychic dominants which have been shown to exist in fish populations by Newman (1956) and Brown (1946); the existence of intraspecific social orders is supported by studies of Gerking (1953) and Miller (1954) that showed strong territoriality in stream fishes. A study done by Greene (1952) provides some evidence that selection for timidity does exist; eggs from wild brook trout yielded fry that were very timid and grew poorly compared to fry reared from eggs of brood stock that had been in captivity since 1902. Later, in planting experiments, the wild stock showed better survival.

DISCUSSION

The fishes are unquestionably an active group, evolutionarily speaking, as is borne out by the existence of over twenty thousand species. Nevertheless there is not much concrete evidence that man's influence has been a big factor in speciation or genetic change in fishes.

The main conclusion that must be drawn from this review is that great caution should be exercised in attributing changes in fishes to genetic factors. There is no clear-cut evidence of exploitation having caused any heritable changes in fishes. As a group, fishes are so plastic that a very wide range of environmental conditions is successfully met without selection taking place. Heavily exploited fish populations respond by earlier maturity and increased growth rates and it has been amply demonstrated that such changes are not necessarily entirely genetic. Thus, on cessation of exploitation, growth rates and other characters of the population revert quickly to the pre-exploitation level. This reversion to a

slower growth rate can occur in the individual fishes; it need not be postponed to later generations, thus indicating that no genetic factors are involved. Similarly, unusually heavy populations, which have become stunted, when thinned out, or transferred to new areas (e.g., Greene, 1955 for stunted brook trout), exhibit normal growth potentialities, within the actual fishes remaining after thinning out, or after transfer.

Angling is a highly selective process; it is here suggested that the well-known difficulty of catching brown trout, and their proven greater intelligence may be due to the much greater number of generations that the species has been fished for, compared to other salmonids. Possibly, also, the gradual worsening of angling in heavily fished areas may be due to a gradual increase in wariness of the fish, brought on by angling selection.

Among established populations, even those containing relatively recent, sympatric, sibling species, there exists an extraordinarily effective isolating mechanism. Such hybrids as do occur are of reduced fertility and are strongly selected against. Examples of exotics or hybrids displacing native species are extremely rare and there is ample evidence of the contrary result—the exotic species failing completely to become established. However, there is some evidence that, among salmonids, considerable introgression has occurred. Thus cutthroat trout with some rainbow characteristics are abundant in streams of the Eastern Slopes; conversely, introduced rainbow trout show some unmistakable cutthroat characteristics.

The rather small amount of selective breeding that has been attempted by fish culturists has shown that it is relatively easy to successfully select for such characters as early maturity or fast growth or high fecundity. However, such selected stocks often prove to be selected against in nature due to pleiotropic or linkage effects masked in the artificial hatchery environment. Herein lies a critical difference between fish breeding and live-stock or plant breeding; live-stock and plants are maintained indefinitely under controlled conditions; the fishes *are always returned, usually at young ages, to natural conditions.* The fish breeders' task is thus infinitely more difficult.

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Alterations in the Blood Level of Lactic Acid in Certain Salmonoid Fishes Following Muscular Activity. III. Sockeye Salmon, *Oncorhynchus nerka*[1,2,3]

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ABSTRACT

The blood level of lactic acid in hatchery-raised sockeye salmon, *Oncorhynchus nerka*, was studied following 15 minutes of vigorous muscular activity. Yearling salmon acclimated and exercised in fresh water showed a sevenfold increase in blood lactic acid following activity, increasing still further during the first two hours of recovery, as in the Kamloops trout, *Salmo gairdneri*. Yearling salmon acclimated in sea water for two days and then exercised exhibited higher immediate increase in lactic acid and showed less fatigue. The sea water appeared to aid the yearling salmon in coping with fatigue products. However, two-year-old salmon that had been acclimated a year and a half in sea water showed the same change in lactic acid following exercise as the yearlings in fresh water. Five of 19 two-year-old salmon died following the exercise.

INTRODUCTION

Alterations in the blood level of lactic acid following severe muscular activity have been reported for two salmonoids, namely the Kamloops trout, *Salmo gairdneri* (Black, 1957a) and the lake trout, *Salvelinus namaycush* (Black, 1957b). In these species, the blood lactic acid increased 7- to 10-fold immediately after exercise, and continued to increase for two hours. The blood level subsided 4 to 8 hours after exercise. The time course of the changes is similar to that observed by Secondat and Diaz (1942) for the tench, *Tinca tinca*, but the extent of the changes was much greater in the salmonoids.

During the summer of 1955, a supply of hatchery-raised sockeye salmon fingerlings, *Oncorhynchus nerka*, was made available for study. The blood lactic acid following vigorous muscular activity was studied in fingerlings exercised both in fresh water and in sea water after two days' acclimation.

Early in 1956 a supply of hatchery-raised two-year-old sockeye salmon were studied. The salmon had been held in sea water one and a half years. A number of these salmon were vigorously exercised in sea water. Blood lactic acid level was followed for 8 hours after vigorous activity. The results of the study will be compared and contrasted with the observations reported previously on the Kamloops and lake trout.

METHODS

The sockeye salmon in this study were reared in the experimental laboratory of the Fisheries Research Board at Nanaimo. In the study carried out in 1955, the fingerlings were transported to the laboratory of the Institute of Fisheries,

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University of British Columbia. During 1956 the sockeye salmon were subjected to fatigue and allowed to recover in the Nanaimo laboratory, where the blood samples were taken, analyzed for hemoglobin, and aliquots removed for protein precipitation. The tungstic acid protein filtrates were transferred to the Institute of Fisheries in Vancouver where they were analyzed the following day.

Hemoglobin was analyzed as acid hematin, and the Barker-Summerson method was used for the analyses of lactic acid. The exact procedures used were taken from Hawk *et al.* (1949).

The method of exercising fish was the same as that employed in the previous studies (Black, 1955, 1957a, b). The fingerling sockeye salmon were continuously exercised for fifteen minutes in a long trough containing sea-water 26.7 grams per kilogram salinity at a temperature 8–12°C. and pH 7.1. The two-year-old fish were exercised in a circular tank in water.

Recently Philips *et al.* (1957) have shown that the percentage of water, protein and fat differ significantly in the hatchery-raised brook trout, *Salvelinus fontinalis*, from wild trout. Wales (1944) has found that the composition of the diet is important in the survival of trout. It is admitted that both the condition of captivity and the nature of the diet may have influenced findings described in in the present paper.

RESULTS AND DISCUSSION

I. Studies on Fingerling Sockeye Salmon, 1955

The hemoglobin levels for the various conditions are presented in Table I. The hemoglobin level following acclimation in sea water has not changed from the level for the fresh water condition. While changes have occurred for both fresh water and salt water conditions following exercise and during recovery, these changes do not differ significantly.

The blood lactic acid level in the unexercised condition was 16.9 mg.% (milligrams per 100 ml. whole blood) in fresh water and 24.1 mg.% in sea water. The

Table I. Average weights and average blood levels of hemoglobin and lactic acid in sockeye salmon fingerlings following vigorous muscular activity. The standard error of the average is given after the average. The number of observations is given in parentheses below the average. Temperature, 8 to 12° C. (= 46.5°-53.5° F.). 1955.

Condition	Average weight	Average hemoglobin	Average blood lactic acid
	g.	*g.%*	*mg.%*
Unexercised			
Fresh water	40±4.27 (11)	8.32±0.89 (9)	16.9±2.19 (10)
Sea water	32±7.17 (11)	8.18±0.95 (6)	24.1±3.32 (11)
Exercised 15 mins.			
Fresh water	36±4.5 (10)	9.37±0.66 (9)	112±4.8 (10)
Sea water	45±4.48 (10)	11.1±1.19 (8)	167±9.4 (10)
Recovered for 2 hours after exercise			
Fresh water	33±2.08 (10)	9.25±0.41 (8)	211±15.2 (10)
Sea water	36±5.56 (11)	7.33±0.6 (9)	117±30.6 (11)

increased level in sea water was borne out by the obvious increased activity of the fingerlings in the sea water acclimation tanks. The unexercised value for the fresh water phase is similar to that observed for fingerling Kamloops trout, which was 15.7 mg.% (Black, 1955).

Immediately following 15 minutes of exercise, the lactic acid of blood of sockeye in fresh water increased to 112 mg.%, whereas sea water acclimated sockeye increased to 167 mg.% (Table I). It should be noted that the sea-water salmon did not appear to be fatigued at the end of the 15 minutes exercise. Furthermore, it did not appear to be difficult to obtain blood samples from the fish in sea water.

It is unlikely that the level of glycogen in the muscle has increased sufficiently in the sea-water acclimated fish to account for the significantly higher blood level of lactic acid.

The level of blood lactic acid of fingerling sockeye following exercise in fresh water is of the same order noted for Kamloops trout fingerlings, 99.8 mg.% $\pm$ 0.95 (Black, 1955).

Following two hours of recovery from vigorous exercise, the fresh-water blood level increased from 111 to 210 mg.% (Table I). In contrast, the sea-water values declined from 167 to 117 mg.%. Indeed, if one very high value, namely 368 mg.% were taken from the two-hour recovered sea-water series, the average value would be 80 mg.% following recovery in sea water.

It should be noted here as well that the fish swam continuously in sea water during the recovery period.

Response of the blood level of lactic acid in the fingerling sockeye salmon exercised in sea water corresponds very closely to the changes observed in the yearling Kamloops trout (Black, 1957a).

The concentration of blood lactic acid in sea-water fingerlings is significantly higher than that for fresh-water fish immediately following exercise. The blood level of lactic acid following two hours of recovery is significantly lower in the sea-water fingerlings compared with the fresh-water fingerlings. Coincident with these facts was the observation that the fingerlings in sea water did not appear to be fatigued during exercise and were very active in the holding tank during the recovering period. Furthermore, the blood samples were much easier to take than in the fresh-water fish. The interpretation of these facts is that in some way cardiac activity and the circulation of the blood was more active in the sea-water fish than in fresh-water fish during and following severe muscular fatigue.

It is probable that the hydrogen ion of the lactic acid was exchanged through the gills for a basic cation. Indeed, the lactic acid may also have been excreted through the gills in the fish exposed to sea water. Further confirmation of the view that salt water may be of benefit to fish exhausted through exercise in fresh water is provided by Bates and Vinsonhaler (1957). They showed that 90% of the striped bass (*Roccus saxatilus*) and salmon (*Oncorhynchus tshawytscha*) which had been exhausted from swimming recovered when transferred from fresh water to salt water, but died if left in fresh water. However, shad (*Alosa sapidissima*) in similar conditions did not respond well to the salt treatment.

II. Studies on Two-Year-Old Sockeye Salmon, 1956

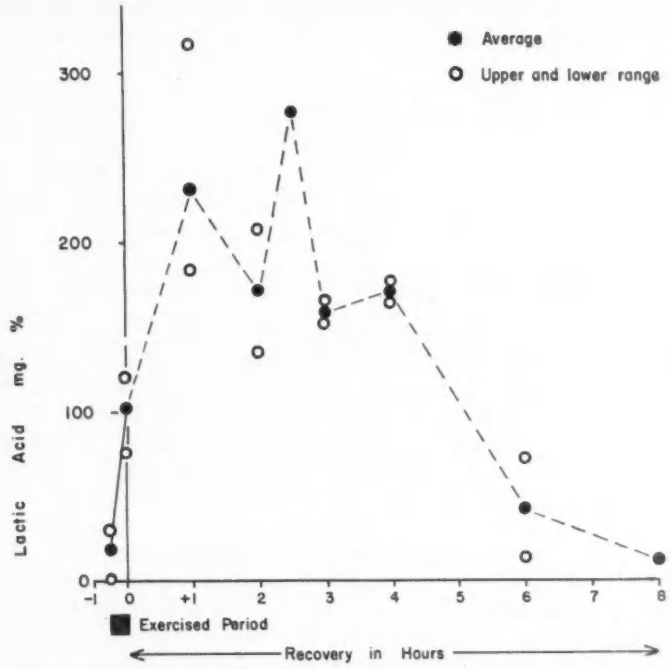
A. effects of muscular exercise. The effects of muscular exercise on blood level of lactic acid in two-year-old sockeye salmon exposed to sea water for one and a half years are presented in Table II and illustrated in the accompanying Figure. The true values of lactic acid for the unexercised condition are probably much lower than the average of 19.5 mg.%, for in the very small sample of five observations three values were below 12 mg.% and the other two were above 29 mg.%.

The average blood level of lactic acid immediately following vigorous activity was 103 ± 6.39 mg.%. This value is of the same order as that noted for the fingerling sockeye salmon exercised in fresh water, but significantly lower than the value for the fingerlings immersed in sea water for two days (Table I). The variability is low in view of the variability of muscle glycogen content observed in spring salmon, *O. tshawytscha,* by Greene (1921) and in Atlantic salmon, *Salmo salar,* by Fontaine and Hatey (1953).

The course of recovery following exercise is presented in Table II and illustrated in the Figure. The results compare very closely to those obtained for the Kamloops trout (Black, 1957a) and the lake trout (Black, 1957b). There was a marked increase in the blood level of lactic acid after the end of the exercise period. From the few data obtained, it would appear that the lactic acid began to subside after three hours of recovery. However, as for the other salmonoids, the value did not subside to levels approaching the initial resting condition until after six hours of recovery.

Table II. Condition, weights and blood levels of hemoglobin and lactic acid of 2-year-old sockeye salmon following severe muscular exercise for 15 minutes in sea water at 20° C. (= 68.0° F.). 1956.

Condition	Weight	Hemoglobin	Blood lactic acid
	g.	*g.%*	*mg.%*
Unexercised			
Average	193±13.2 (5)	9.54±0.73 (5)	19.5±24.4 (5)
Range	110–338	6.9–11.6	4.7±45.2
Exercised 15 minutes			
Average	188±21.7 (8)	11.6±0.38 (8)	103±6.39 (8)
Range	150–330	9.8–13.3	76.5–121
Post-recovery			
1 hour	119	12.3	316
1 "	198	11.8	184
1 "	395	8.3	192
2 hours	242	12.2	208
2 "	154	8.5	135
2.5 "	191	13.2	278
3 "	250	8.1	152
3 "	240	9.3	164
4 "	340	10.1	165
4 "	220	8.8	177
6 "	230	11.4	72.6
6 "	170	9.1	13.0
8 "	180	11.1	12.4
8 "	115	10.1	11.8



Alterations in blood level of lactic acid following 15 minutes of severe exercise, and recovery, in two-year-old sockeye salmon in sea water at a temperature of 20°C.

The same explanation for the significant increase of lactic acid above the relatively high level immediately following exercise of the sockeye salmon is offered as that given to explain similar changes in the Kamloops and lake trout (Black, 1957a, b). It is presumed that the lactic acid is produced as the result of chemical changes in glycogen stored in the muscles during activity. It is also presumed that the lactic acid diffuses slowly from the muscles to the blood due to the lower temperature co-efficient (Johnson *et al.*, 1945).

It is not known to what extent salmon under natural conditions would continue to exercise vigorously. However, should the exercise approximate that induced under the experimental conditions, it is obvious that the fish would not recover completely from fatigue for several hours.

B. DEATH RESULTING FROM SEVERE MUSCULAR EXERCISE. Not all the fish subjected to vigorous exercise for fifteen minutes survived during the recovery period. At the end of an hour's time, three fish had died and two more died by the end of the second hour (Table III). In all, five of the nineteen fish that had been vigorously exercised expired following exercise. The fourth fish was actually removed from the water before it had stopped breathing. However, all respiratory movements had ceased by the time the blood sample was taken. Blood samples were drawn from each fish before *rigor mortis* had set in.

TABLE III. Time of death during recovery, weights and blood level of hemoglobin and lactic acid of 2-year-old sockeye salmon following severe muscular exercise in sea water for 15 minutes at 20° C. (= 68.0° F.). 1956.

Time of death after exercise	Weight	Hemoglobin	Blood level of lactic acid
hours	*g.*	*g.%*	*mg.%*
1	285	12.2	241
1	129	12.6	292
1	131	10.8	244
1½	251	12.6	208
2	205	12.3	214
Average	200	12.1	240
Standard error	±31.4	±0.34	±14.9

The hemoglobin levels are not significantly different from the average for the fourteen individuals of the recovery series (Table II). The average lactic acid value is 240 mg.%±14.9 (Table III). The average lactic acid for three samples drawn at the end of one hour recovery and two samples drawn at the end of two hours recovery was 207±29.9 with a range of 135–316 mg.% (Table II). The lactic acid values for the five fish which expired, while higher, are not significantly different from those that still appeared to be in good condition.

There are factors other than blood lactic acid which may have contributed to the death of these fish. As von Buddenbrock (1938) first observed, the blood in the gills of these fatigued fishes was very dark, indicating that the oxygen transport was reduced. Secondat (1950) also showed that the oxygen capacity of carp blood was reduced as a result of muscular exercise. Auvergnat and Secondat (1942) also showed that the carbon dioxide content of the blood of carp is reduced as a result of muscular activity. While the temperature at which the experiments were carried out was below the lethal temperature, nevertheless the temperature was probably higher than the average condition for open sea water. Finally, some scales were lost by most of the fishes in this experiment as a result of the exercising and handling procedures. However, no careful account was made at the time of the number of scales lost. Extensive loss of scales may, however, be a principal condition causing mortality, as noted by Vernon D. van Someren during tagging of Atlantic salmon smolts in Scotland (personal communication).

Secondat and Diaz (1942) showed for tench which had been severely exercised that the blood levels of lactic acid increased. They also showed that death followed 12 or more hours later in the three or four fish in which the blood levels of lactic acid failed to decline during the first 6 hours of recovery. While it may not be possible to prove that the endogenous production of lactic acid as a result of severe muscular exercise is the primary cause of death in these salmon, it would appear safe to state that muscular activity and lactic acid are significant correlates of a condition resulting in death. The data presented here substantiate and expand the findings of von Buddenbrock (1938), Huntsman (1938), and Auvergnat and Secondat (1942) that fish may die as a result of severe muscular exercise. Recently A. C. DeLacy and G. J. Paulik (personal

communications) found that mortalities occurred in adult sockeye salmon following severe muscular exercise. The exercise was induced after the fish had been held in fresh water for a month.

In Section I it was found that sea water appeared to be of some benefit to yearling sockeye salmon subjected to severe muscular activity. The suggestion was put forward that this benefit may be due to exchange of lactic acid by the gill for a neutral salt. This benefit, if it really exists, appears to be completely lost by fish exposed to sea water for 1½ years. It will be interesting to determine the effect of exercise upon mature salmon after they return from the sea to fresh water.

Whatever the true cause of death following severe muscular activity the implications of muscular activity to survival are important, especially in the study and management of fishes. In tagging experiments, fish should be subjected to the least possible degree of exercise and handling. Furthermore, fish which have been caught by hand lines or by trolling may expire subsequently as a result of the muscular exercise. If the latter proves to be the case for all sizes of salmon, fishing regulations regarding the size of fish to be thrown back into the water might be reviewed.

SUMMARY

1. There were no significant changes in the blood level of hemoglobin following exercise and recovery for either fingerling or two-year-old sockeye salmon.

2. The blood level of lactic acid in fresh-water fingerling sockeye exercised for fifteen minutes was 111±4.8 mg.%, as compared with 16.9±2.2 mg.% for the rested condition, and 210±15.2.mg.% after two hours of recovery. These changes are similar to those reported for Kamloops and lake trout.

3. The blood level of lactic acid for fingerling sockeye salmon acclimated for two days in sea water was 24.1±3.32 mg.%. Following fifteen minutes of vigorous activity in sea water the blood level increased to 167±9.4 mg.% and then decreased to 116±30.6 mg.% following two hours of recovery. Correlated changes in behaviour indicated that sea water appeared to be of immediate benefit to fingerling sockeye salmon in coping with the metabolites of muscular exercise.

4. Two-year-old sockeye salmon which had been reared in laboratory conditions showed a blood level of lactic acid of 19.5±24.4 mg.%. Following fifteen minutes of severe muscular exercise the blood lactic acid increased to 103±6.39 mg.% and then increased still further to 172 mg.% during the first two hours of recovery.

5. During the recovery period the blood level of lactic acid continued to increase during the first hour of recovery and did not decline to approach the resting level until the sixth hour of recovery. These changes are similar to those reported for Kamloops and lake trout.

6. During the recovery period, five out of nineteen fish died between the first and second hour of recovery. The average level of blood lactic acid for the

fish which died was 240±14.9 mg.%. The benefit of sea water to the fish after exercise appears to have been lost. Indeed, the fish are more susceptible to death following exercise than salmon exercised in fresh water.

7. The implications of severe muscular exercise to the biology and management of the fishery of sockeye salmon are discussed briefly.

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Reactions of Juvenile Pacific Salmon to Light[1,2]

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ABSTRACT

When given a choice between light and dark areas, schools of chum or pink salmon fry remain in the light, sockeye fry prefer the dark and coho fry show no marked preference for either. Newly emerged sockeye fry are the most strongly photonegative, remaining mostly under stones. Older sockeye fry move more into the light. Sockeye and coho smolts stay in the dark more than sockeye and coho underyearlings. Territorial and "escape" behaviour by fish in the experimental apparatus may obscure these reactions to light. Soon after emerging from the gravel, pink fry swim near the surface under low light intensity and retreat to deeper water in brighter light. Older pink fry seem indifferent to changing light. Recently emerged chum salmon fry do not respond in this way to changing illumination, although older fry tend to swim closer to the surface. This difference between pink and chum salmon fry may be related to differences in schooling behaviour and alarm responses of the two species.

INTRODUCTION

In a horizontal light gradient, with intensity ranging from 28 foot-candles to less than one ft-c., chum salmon fry (*Oncorhynchus keta*) were found to prefer the brightest areas while coho fry (*O. kisutch*) and sockeye fry (*O. nerka*) preferred the darkened ones (Hoar, MacKinnon and Redlich, 1952; Hoar, 1954). These reactions were in agreement with many different laboratory tests and were assigned a prominent role in the postulated mechanism for the seaward migration of chum salmon fry and the lake residence of sockeye fry (Hoar, 1954). It was suggested that chum salmon fry move into brighter areas of fast water during the day and are displaced downstream at night when rheotactic responses are reduced at lowered light intensities. The residence of juvenile sockeye salmon in lakes was attributed to their preference for the low light intensities which exist in deeper waters. It was postulated that the responses of pink salmon fry (*O. gorbuscha*) to light would be similar to those of chum fry since much of their general behaviour is the same.

It has been pointed out (Neave, 1955) that the postulated mechanism for pink and chum migration is at variance with field observations. Under natural conditions pink and chum salmon fry are rarely seen during the day, and it has now been established (Hoar, 1956) that the reactions described in earlier papers were those of schooling fish and that, while in the rivers, pink and perhaps also chum fry behave as individuals rather than schools.

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Several points still require clarification. It may be assumed that the migration of pink and chum salmon fry through many river systems requires several days. If they are not to be seen during such periods, there must be some mechanism related to light intensity which will bring them out of the river bottom at night and take them as individuals into it at dawn. An attempt was made to demonstrate some such mechanism by observing the fish in deep water under a series of light intensities. The photo-responses were also re-investigated for another reason. The maximum illumination used in earlier experiments was of an intensity (28 ft-c.) which, in nature, only prevails in the early morning and evening. The observations reported here were made at intensities ranging to those often found at midday in the natural habitat (1,000 ft-c.).

Four species of *Oncorhynchus* (*keta, gorbuscha, kisutch* and *nerka*) have been studied under identical conditions and an attempt made to present a comparative picture of their photo-responses and to relate these to their other behaviour patterns during the juvenile fresh-water stages. It was hoped that the experiments would lead to a more precise evaluation of the role of light in governing the juvenile fresh-water behaviour of these species.

MATERIALS AND METHODS

The experiments were carried out in dark rooms under controlled illumination in the spring and summer of 1953 and 1954. Fish were hatched at the University or collected from several different streams of the lower mainland of British Columbia. Size of fish and pertinent temperature data are given in connection with the various experiments. Fish were retained and fed under conditions comparable to those of previous investigations (Hoar, MacKinnon and Redlich, 1952; Hoar, 1954).

PREFERENCE FOR ILLUMINATED OR DARKENED HALF OF AN AQUARIUM. Two series of experiments were performed with the four half-darkened aquaria illustrated in Figure 1. In the first series 75-watt reflector lamps were used and connected through a rheostat to provide light intensities of 10, 45, 80, 115 and 150 ft-c. measured at the water surface under the lamp. In the second series a constant illumination of 500 ft-c. was provided by 500-watt photoflood lamps.

In the experiments with changing light intensity 10 fish were placed in each aquarium and the room left in darkness for one hour. Illumination was then increased to 10 ft-c. and the distribution of fish, with respect to the light and dark halves of each aquarium, recorded at one minute intervals for 10 times. The illumination was then abruptly increased to 45 ft-c. and another 10-minute record made. This was repeated at 80, 115 and 150 ft-c. The 150 ft-c. illumination was maintained for 30 minutes, followed by a 10-minute record of the distribution of the fish and a repetition with the changing series of intensities in decreasing order. Fish now remained in complete darkness for one hour and were then suddenly exposed to 150 ft-c. for a 10-minute record of distribution. They were then returned to the holding tanks. Numbers of replications appear in the tables of results. For comparative purposes at least two species were always observed at the same time.

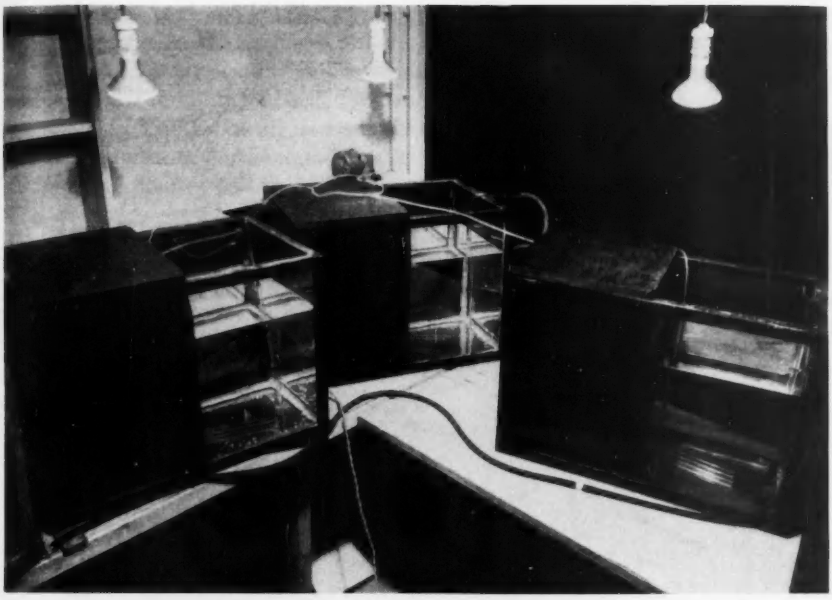

FIGURE 1. Four identical aquaria (75 litres capacity, containing 55 litres of water) used to measure response to light. Half of each aquarium was blackened on the outside with "Tygon" black paint, and was covered with a light-tight black cover which extends downwards across the middle of tank to the water level. Cold water circulating through glass tubes prevented warming of the water by electric lamps. Not shown in the photograph were plywood partitions between the different aquaria, to prevent scattering of light from one experiment to another.

In the experiments with constant illumination of 500 ft-c., ten fish were placed in each aquarium and left for one hour in darkness as before. The lights were suddenly set at full intensity and distribution recorded every 30 seconds for 30 minutes. Fish were then returned to the holding tanks.

EFFECT OF HIGH LIGHT INTENSITY COMBINED WITH WATER CURRENT AND TURBULENCE. Four rheotaxis tubs, previously described and illustrated (Keenleyside and Hoar, 1954), were used in a manner comparable to the aquaria described above. The interior was coated with aluminum paint and in two of the four tubs the bottom was covered with stones and gravel. Light-proof wooden covers extended over half of the tub and vertically downward across the middle almost to the water level. The 500-watt photoflood lamps were adjusted so as to produce a maximum illumination of 1,000 ft-c. at the exposed water surface. Water flow of 25 to 30 cm./sec. at the periphery was maintained in two of the tubs (in one with stones and gravel and in one without). No flow was produced in the other two tubs. Either 12 fry or 6 smolts were placed in each tub under full light intensity and left undisturbed for 15 minutes. The numbers of fish in the light and the dark halves of each tub were recorded

10 times at one-minute intervals, the light reduced to 500 ft-c. and a second record made. A third record was made at 5 ft-c. Fish were then left in darkness for 30 minutes and the series repeated in ascending order.

MOVEMENTS IN A VERTICAL LIGHT GRADIENT. The 180-cm. high water column has been described (Hoar, 1954, p. 80–81) and is illustrated in Fig. 2. Stones were placed on the bottom of the tank. A small amount of water circulated in

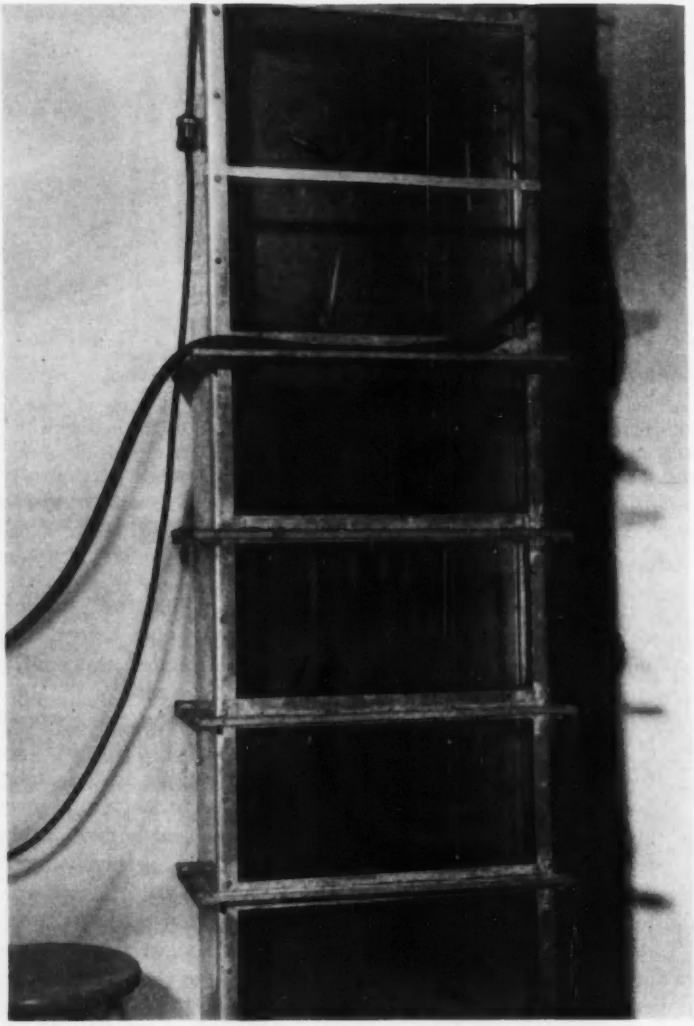

FIGURE 2. Photograph of a tank 180 cm. high, 60 cm. wide and 22.5 cm. from front to back. Construction is of sheet aluminum with a plate glass front.

at the bottom and out the top to maintain an even temperature. This did not create any rheotactic responses in the fish. The maximum illumination at the surface was 1,000 ft-c. and by means of a rheostat was varied to provide the series 1,000, 500, 100, 50, 10 and 5 ft-c.

Groups of 24 fry or 12 smolts were placed in the tank during the afternoon of the day prior to first observation. Next morning, illumination was set at 1,000 ft-c. for 30 minutes and then the distribution recorded with respect to 6 equal horizontal areas of the tank, at one-minute intervals for 10 times. Illumination was then changed to 500 ft-c. and a second record made. The above series of intensities was thus used in order; the fish were then left in total darkness for 30 minutes and the series repeated in ascending order. Lights remained on at full intensity for one hour and the whole procedure was repeated during the afternoon. The same group of fish was used for two successive days and then discarded. Careful notes on behaviour of the fish were made throughout.

RESULTS

Responses to Intensities Ranging from 0 to 500 foot-candles

The responses of salmon in the half darkened aquaria (see Fig. 1) when subjected to changing illumination are tabulated in an abbreviated form (Table I). Because of the many figures involved, values are given for only 5 of the 11 intensities, *viz.* the initial minimum intensity of 10 ft-c., the maximum intensity of 150 ft-c. on the ascending series, the value for the same intensity after an exposure of 30 minutes; the minimum intensity of 10 ft-c. on the descending series and the result of sudden exposure to 150 ft-c. after one hour in the dark. These selected values show essentially the same picture as the complete tabulation of the data—probably because the fish's eye adapts to the changes much more rapidly than light intensities were altered.

Table I shows several characteristics and differences in the responses of the species. In no case is the response of the all-or-none type. Young salmon, under these conditions, do not hide in the darkened area or remain constantly in the illuminated area. They are continuously on the move passing to and fro from one area to the other, in some cases showing schooling behaviour, in others nipping, chasing and territorial reactions. The maximum values recorded were 84.9% chum fry *in the light* at 80 ft-c. (not shown in Table I) and 74.5% sockeye smolts *in the dark* under 150 ft-c. In general, however, the responses range 10% to 20% above or below the 50% uniform distribution value. Another point of general interest arising from Table I is the fact that the series of values which throughout shows the highest degree of statistical significance is that obtained on sudden exposure to 150 ft-c. after one hour in darkness. Stimulation from the abrupt change produces consistent results not always observed when the eye has time to adapt.

At these intensities, pink and chum salmon fry are uniformly photopositive. In the 33 P-values recorded, the only one rising above 0.01 was the value of

TABLE I. Numbers of salmon in the illuminated half of an aquarium (see Fig. 1), of the total of 100 in the aquarium. The total number of positions plotted for each light intensity is equal to the number of tests × 100. The *t* and P values are for the differences between the mean number of fish in the two halves of the aquarium; means are based on 10 tests except in case of pinks (12 tests), with 10 fish in aquarium.

	Illumination at water surface—*foot-candles*				
	10	150	150	10	150
O. gorbuscha—wild stock Nile Creek 2.5 to 3.5 cm. May 8–14					
Mean	62.1	60.9	63.3	74.8	38.6
t	5.042	2.535	3.410	12.098	6.909
P	<0.01	0.02	<0.01	<0.01	<0.01
O. keta—hatchery stock 5.6 cm. May 8–20					
Mean	79.7	69.5	68.5	61.0	68.6
t	14.488	11.471	7.255	7.091	7.294
P	<0.01	<0.01	<0.01	<0.01	<0.01
O. keta—wild stock Nile Creek 4.5 cm. May 11–21					
Mean	79.1	71.6	80.5	68.1	59.1
t	15.316	5.468	12.708	6.704	2.984
P	<0.01	<0.01	<0.01	<0.01	<0.01
O. nerka—hatchery 2.3 cm. May 30–June 4					
Mean	58.9	38.4	45.1	51.7	43.7
t	4.811	4.000	1.463	0.895	2.930
P	<0.01	<0.01	0.17	0.38	<0.01
O. nerka—hatchery 2.6 cm. May 25–June 3					
Mean	65.0	41.2	45.6	59.1	61.2
t	6.250	4.293	1.630	3.500	4.00
P	<0.01	<0.01	0.13	<0.01	<0.01
O. nerka—Cultus Lake 10.0 cm. May 9–23					
Mean	50.9	42.9	40.1	45.3	35.5
t	0.375	2.448	11.980	2.136	20.417
P	>0.5	0.03	<0.01	0.05	<0.01
O. nerka[a]—Cultus Lake 11.7 cm. July 16–17					
Mean	22.4	22.8	24.4	27.3	14.5
t	1.238	1.467	0.316	1.070	6.000
P	0.24	0.17	0.5	0.3	<0.01
O. kisutch—Salmon and Brunette rivers 3.9 cm. May 25–31					
Mean	68.3	54.5	51.7	63.5	49.4
t	6.203	1.875	0.354	3.971	0.218
P	<0.01	0.08	0.5	<0.01	>0.5
O. kisutch—Nile Creek 8.0 cm. May 9–27					
Mean	43.2	32.6	34.3	34.7	32.9
t	1.971	4.703	4.078	4.935	5.797
P	0.07	<0.01	<0.01	<0.01	<0.01

[a]Only 5 fish per group and 8 tests. Mean in dark = 50 − mean in light.

0.02 recorded for pinks in Table I under 150 ft-c. The results are unusually consistent and leave little doubt that this is the reaction of schooling chum and pink salmon fry at this age and under these relatively low intensities of illumination. The data conform with earlier studies for chums in aquaria (Hoar, MacKinnon and Redlich, 1952; Hoar, 1954) and for schooling chums and pinks in streams and rivers (Hoar, 1956).

Coho fry are less consistent in their response. At light intensities of 10 ft-c. and 45 ft-c. the numbers in the light were significantly greater than those in the

dark. At higher intensities, however, the fish either retreat or become indifferent to light and are about equally distributed between the two areas. This behaviour is in line with their rapid adaptation to current (MacKinnon and Hoar, 1953) and to alarming stimuli (Hoar, unpublished). Coho smolt display a marked and uniform negative response.

In general, the negative phototaxis previously described for juvenile sockeye was evident although less marked under laboratory than under outdoor illumination (Hoar, 1955). The smallest (youngest) fry studied avoided the light more markedly than the larger and older fry. In fact more than 50% of the older fry were under the light in seven out of the 11 intensities. This happened with the younger fry only at low intensities (10 ft-c., Table I). Although the results are somewhat irregular with the changing series of intensities, the sockeye smolt displayed the most strongly marked negative response of any group when suddenly exposed to 150 ft-c. illumination.

Table II shows the 30-minute response of three species when suddenly exposed to illumination of 500 ft-c. Although the results are in general similar to those obtained at 150 ft-c. the retreat of the fish from the more intense illumination is evident. The percentage values are usually lower than those recorded in Table I. The rather variable results obtained with different groups of sockeye smolt were obviously due to the marked activity of the animals in the limited space.

TABLE II. Percentage of fish in the illuminated half of an aquarium during 30 minutes following sudden illumination of 500 ft-c. Corresponding *t* and P values are for differences between the mean numbers in the illuminated and the dark areas of aquarium. The first six groups of ten fish each were tested June 16–20, with temperature range 11–13° C.; the last groups were tested July 9–15, with temperature range 13–16° C.

		Length *cm.*	Tests	% in light	*t*	P
Fry	chum	5.6	8	56.5	3.529	<0.01
,,	coho	3.9	6	39.0	3.657	<0.01
,,	sockeye	2.3	6	42.8	3.639	<0.01
,,	sockeye	2.6	6	48.3	0.928	0.38
Smolts	coho	8.0	4	12.5	40.214	<0.01
,,	sockeye	10.0	6	50.0	0.012	>0.50
Smolts sockeye						
,,	2 fish/group	11.7	5	46.8	0.585	>0.50
,,	4 fish/group	...	...	32.7	4.782	<0.01
,,	5 fish/group	...	...	29.3	9.920	<0.01
,,	6 fish/group	...	...	38.1	1.448	0.19

RESPONSES TO INTENSITIES RANGING FROM 0 TO 1,000 FOOT-CANDLES

This group of experiments was designed to test responses to light under conditions more nearly comparable to those in nature. A group of 4 tubs in which circular rotating currents could be produced were substituted for the aquaria and the maximum light intensity raised to 1,000 ft-c. In addition, stones were placed in the bottom of two of the tubs (one with and one without flowing

TABLE III. Illumination in foot-candles recorded at Port John, B.C., May 1–15 inclusive, 1955, as measured by an exposure photometer, Model 200, Photovolt Corporation, New York.

	Time of day—Pacific standard time				
	6–7	9–10	Noon	15–16	19–20
Mean, *ft-c.*	270	1270	1750	1330	98
Range, *ft-c.*	30–1000	250–2500	530–3500	375–3500	10–220

water) to increase turbulence and provide additional cover. The light intensity of 1,000 ft-c. approached light conditions in nature. In Table III mean light intensities are recorded for the period of active juvenile salmon migration at Port John in 1955. Since young fish are found at varying depths in rivers and lakes the intensity of 1,000 ft-c. at the surface of the relatively shallow (17.5 cm.) tubs approaches daytime light intensities where the fish are found in nature.

One group of each type of fish was studied in each of the four tubs. Consequently, replications are not available for a presentation of data comparable to Table I. The reactions of the fish are recorded in terms of percentage of fish appearing in the exposed area during the period of observation (Table IV). For this purpose the two readings at 500 ft-c. and the two at 5 ft-c. were combined.

A comparison of Table IV with Tables I and II shows that the percentage of fish in the exposed area is usually less in this experiment than it was when maximum intensities reached only 150 ft-c. or 500 ft-c. Interpreted in terms of 50% response, all groups are now photonegative. Although the entire apparatus is different, it seems reasonable to conclude that this difference is due to the brighter light. In support of this it may be recalled that the number in the exposed area of the aquaria was less when illumination was increased from 150 ft-c. to 500 ft-c. (Tables I and II). In the present experiments the fish are first exposed to the highest intensity and their initial retreat beneath the cover may reduce their tendency to emerge even at lower intensities if they have become related to that particular locality.

Differences are evident in the pattern of the responses of the various species. When the percentage values are compared (Table IV), chum and sockeye fry and sockeye smolt show a marked tendency to retreat under strong light or to emerge at low light intensity. The reverse picture is evident with pink, coho fry and coho smolt. The smolt groups are less consistent than the fry in this regard.

The presence of turbulent flowing water produced little or no effect on the distribution of fish (Table IV). Small differences may be attributed to drifting of fish from one area to the other but the general pattern of distribution is unaltered by the currents. It was evident that fish held position more strongly when rocks were present. Without rocks they drifted more frequently and in the cases of pinks swam with the current.

The presence of stones may have modified the distribution of the coho fry and to a lesser extent the chum fry. In five out of six cases coho and chum fry emerged in larger numbers when stones were present. Such behaviour is probably related to their habit of living over the bottom of a stream and to their responses to cover when alarmed.

TABLE IV. Percentage of fish in the exposed area of a tub. Distribution was recorded at 10 one-minute intervals, with groups of 12 fry or 6 smolts. In each case the percentage is based on 4 such records (40 minutes) for 500 ft-c. and for 5 ft-c., and on 2 such records (20 minutes) for 100 ft-c.

Conditions in tub	Illumination	Pink fry	Chum fry	Sockeye fry	Coho fry	Coho smolts	Sockeye smolts	Total fry
	ft-c.	%	%	%	%	%	%	%
Current, no rocks	5	36.5	44.8	61.3	32.9	54.2	45.8	44.1
	500	45.8	30.3	15.0	47.1	54.2	49.6	33.7
	1,000	46.3	32.5	11.3	49.6	36.7	42.5	34.4
Current, rocks	5	46.3	45.6	35.4	35.0	36.3	50.0	41.6
	500	45.2	30.7	16.3	53.9	41.3	50.8	35.4
	1,000	51.7	22.3	13.3	43.8	40.8	39.2	30.7
No current, no rocks	5	27.1	51.7	47.5	23.5	17.5	34.6	40.3
	500	33.8	29.1	21.7	38.1	18.3	51.3	30.3
	1,000	51.7	21.0	32.5	41.7	25.0	57.2	33.6
No current, rocks	5	37.9	66.3	45.2	37.9	37.5	40.8	50.7
	500	31.5	34.0	38.3	50.8	41.3	34.2	37.7
	1,000	40.0	38.5	29.6	48.3	49.5	27.5	39.0

MOVEMENT IN A VERTICAL LIGHT GRADIENT

Figures 3 and 4 show the changing distribution of fish in three areas (top 30 cm., middle 60 cm. and bottom 30 cm.) of the 180 cm. tank under the 6 different intensities of illumination. Although a 1.5° to 2.5°C. gradient existed from bottom to top of the tank, temperature conditions were uniform in these areas and the changing picture within any area should not be biased by temperature effects.

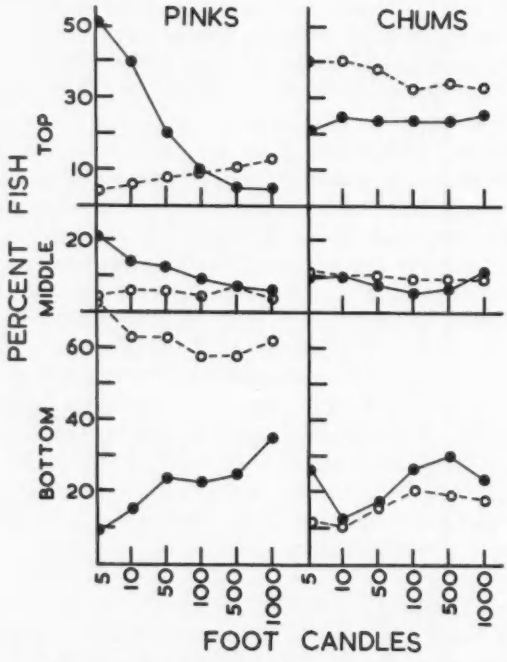

FIGURE 3. Distribution of pink and chum fry in three areas of the vertical tank under different intensities of illumination. Solid line, wild fish (May 5 pinks and May 27 chums); broken line, hatchery fish (July 6 pinks and May 19 chums). Each point is an average of 10 trials with May 5 pink fry and with all chum fry, and of 8 trials with July 6 pinks. Samples were of 24 fish; light intensities were measured at the surface.

A marked change in behaviour of pink fry occurred between May and July. Pink fry studied in May were captured as downstream migrants in Nile Creek on May 1 and tested in the vertical tank on May 4 and 5. They were migrating schooling fish (Hoar, 1956). This same stock of fish was tested again after two months. In May, pink fry move out of the upper areas of the tank into the lower areas as the light intensity increases. The movement is clearly an

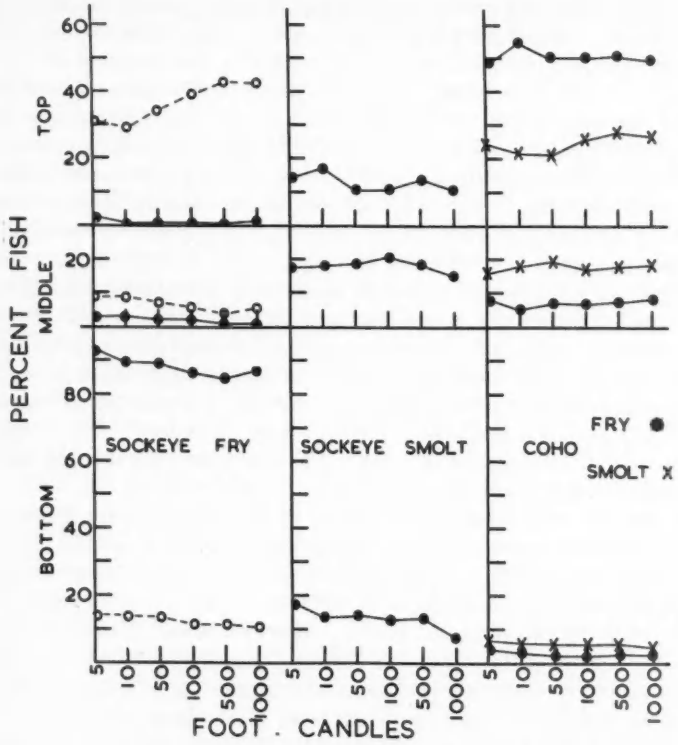

FIGURE 4. Distribution of sockeye and coho in three areas of the vertical tank. Each point is a mean value for 8 trials at that intensity, except in the case of coho smolts which were tested 12 times. Sockeye fry, solid line on May 11; sockeye fry, broken line on July 23; sockeye smolts, August 3; coho fry, May 31; coho smolts, June 11.

orderly one directly related to light intensities. At 5 ft-c. pinks frequently swam directly into the surface film of water as observed during their nocturnal migrations (Neave, 1955). Pink fry were never seen to go under the stones at bottom of the tank. Although the trend lines are reversed in July the response to the gradient is so slight that it seems best interpreted as an indifference to changing illumination. Schooling seemed less compact in the July tests and the fish were never observed swimming into the surface film.

The chum fry tested on May 27 had been procured two days previously from Nile Creek as downstream migrants. Those tested on May 19 were hatchery reared fish—several weeks past the time when they would probably have migrated in nature. The contrast between the two groups is not particularly great. It is indicated, however, that the older (May 19) fish are nearer the surface than the younger migrants (May 27). In strong contrast to the pink fry there is no marked response to the changing light intensity.

Coho fry and smolts showed no response to the gradient in light intensities (Fig. 4). The contrast between fry and smolts was similar to that previously observed with constant light (Hoar, 1954). Fry are closer to the surface than are the smolt. General observations at the lowest intensities where the fish could be observed showed the fry evenly distributed in the tank and inactive. At about 10 ft-c. activity became evident while at 50 ft-c. and higher they swam rapidly up and down through different levels. They did not take cover under stones nor show aggregating tendencies. Coho smolt swam slowly from one section of the tank to another at all intensities above 5 ft-c. but below this seemed inactive like fry.

The sockeye smolts (Fig. 4) were indifferent to this particular light gradient and behaved in essentially the same manner as they had under uniform lighting. "Sockeye smolts are notably active in all the different experiments, but in the 180-cm. water column their activity is extreme. All individuals swim straight up and down at great speed. They were never motionless during these observations. This activity results in close to random distribution" (Hoar, 1954). This behaviour is now recognized as *escape behaviour* and has nothing to do with the response to light gradient.

The behaviour of the sockeye fry evidently changed during the two-month interval between the earlier and later tests. Fry tested in May remained inactive at the bottom of the tank as previously described for fry under constant light conditions (Hoar, 1954). The provision of stones in the present test permitted one additional observation. Almost all the fry remained under the stones at all light intensities. By turning the lights on suddenly it was evident that they frequently remained under the stones even during darkness. These were the only fish which showed this strong relationship to the bottom cover. Sockeye fry tested in July no longer went under stones and showed a marked tendency to move away from the bottom and into the upper layers at all intensities. In fact the trend line in the top compartment shows an increasing concentration in the top area as light intensity rises. A change from a strongly photonegative toward a photopositive response is evident.

DISCUSSION

Because of the nocturnal migratory habits of juvenile Pacific salmon it is natural to regard them as photonegative—retiring to sheltered places during the day and emerging at night. Indeed, with the exception of coho and spring salmon fry one sees little of the juvenile Pacific salmon during their residence in fresh water. Occasionally, however, under apparently normal conditions all species may be seen—at least in small numbers—in exposed places during the day. The experiments reported here likewise show that the light responses of these fish are never of the "all or none" type. The term "phototaxis" does not seem to be appropriate. Even when exposed to sudden changes in illumination of relatively high intensity the reactions lack the precision of classical taxes or forced movements.

Numerical data, such as those recorded here, must be interpreted with care. For example, sockeye smolts in the 180-cm. tank are uniformly distributed and seem to show an indifference to light (Fig. 4). In fact, however, they show only "escape behaviour" and the reactions observed in this situation are no indication of their responses to light. Again, coho salmon often show aggressive behaviour which results in the dominant individual holding the favoured territory while the subordinates are forced into other areas. In such cases the smallest number of individuals will be in the preferred areas. Numerical data of this type can only be properly interpreted when combined with detailed observations of the activities of the animals. In spite of these limitations the tables and graphs presented here emphasize several facts which are in accord with and add further detail to, the behaviour picture which is being developed for this genus of fish.

Of the schooling fry (sockeye, chum and pink), the sockeye have a much less marked preference for the lighter areas than either chums or pinks. This behaviour of sockeye fry is in accord with their previously described preference for deep water (Hoar, 1954) and shady places (Hoar, 1955).

Even under the most intense illuminations used (1,000 ft-c.) 20% to 40% of the chum fry and up to 50% of the pink fry remained in the exposed areas. A comparison of the reactions of these two species is instructive. In the half darkened aquaria the chum fry showed the stronger preference for light while in the half darkened tubs the preference was stronger with the pink fry. Experience with recently captured migrant fish in the field suggests that there is actually little difference in the photoresponses of the two species. There are, however, marked differences in their reactions when startled or disturbed.

A simple experiment will demonstrate this difference in a striking fashion. Ten fry of each species are placed in separate pails of water. The bottoms of the pails are covered with stones to provide cover. Both groups swim at about the same level in the water whether the pails are placed in bright sunlight or taken indoors. Chum fry, but not pink fry, occasionally swim in among the stones. When startled the chum fry take shelter in the rocks as individuals while the pink fry scatter about above the rocks in a characteristic manner. The reaction can be shown in a dramatic way by simply tapping the rim of the pail. Within 30 seconds the chum fry usually swim out from among the stones while the pink fry group again in an orderly school. Responses to light seem to be similar but there are two very different reactions when suddenly startled. Keenleyside (1955) finds that alarm usually increases the density of the fish school but describes (p. 198) flight reactions among newly hatched rudd (*Scardinius erythrophthalmus*) which seem to be similar to those of the young pink salmon fry. Schools of different species of fish behave somewhat differently when alarmed and Keenleyside (p. 234, 1955) has discussed the possible survival value of some of the observed reactions.

It is always more difficult to interpret the reactions of coho fry to experimental variables since they often show strong territorial behaviour. Careful notes, however, were made on their reactions during the tests and it is believed that the overall picture obtained from the numerical data is a valid one. This is interpreted as an indifference to illumination of the intensities and rates of change

used in these experiments. This indifference seems to be in accord with the behaviour of an animal which is active by day and lives in relatively shallow water. It is also fully in agreement with the coho salmon's relatively rapid adaptation to rheotactic stimuli (MacKinnon and Hoar, 1953) and to alarm stimuli (Hoar, unpublished). The apparent avoidance of light of low intensities (Table V, 5 ft-c.) is probably due to the inactivity which they show at low light intensities (Hoar, 1951). Stringer and Hoar (1955) found that coho fry settle to the bottom of a tank and remain quiet when the light intensity is reduced below 5 ft-c.

The data show clearly that, during the juvenile fresh water existence, Pacific salmon experience definite changes in the magnitude of their response to light. Recently emerged pink salmon fry have a characteristic behaviour of rising to the surface at low light intensities and retreating to the bottom as the intensity rises (Fig. 3). At very low intensities, they may be observed not only rising in the 180-cm. tank but also swimming actively into the surface film. This behaviour of swimming in the surface film of water was described by Neave (1955) in his field studies of pink salmon fry. It is probably an important factor in their migratory behaviour but field observation indicates that the fry may migrate below as well as at the water surface.

The behaviour of "surfacing" at low light intensity probably operates during the early period of active life to keep the fish in the gravel by day and bring them into the surface waters at night. After a time—within two months, and probably much sooner—this behaviour disappears. It should be pointed out that although these schooled pink fry retreated to deeper water as the light intensity was increased they did not take cover under the stones provided at the bottom of the tank. This is fully in accord with observations of schooled pink salmon recorded elsewhere (Hoar, 1956).

The chum fry studied in these experiments did not display the behaviour of changing depth with variations in light intensity (Fig. 3). It is impossible to say whether this is due to species differences in photoreceptor responses, to differences in relative ages with respect to time migration or to fundamentally different behaviour patterns. The photoreceptors of chum fry may be more sensitive to light and adapt more rapidly than those of pink fry. General observation showed that chum fry in the bottom area of the 180-cm. tank were close to the bottom at 0 ft-c. and rose immediately at 5 ft-c. with marked schooling evident between 10 and 50 ft-c. Thus, studies at very low light intensities might show that these apparent differences between the two species are only differences in degree of photosensitivity. On the other hand, although the chums of May 27 were obtained as migrants from Nile Creek it was well after the peak of downstream movement and they may not represent actively migrating fish. Swimming into the surface film at low light intensity was not observed with any of the chum fry studied. Again, as described above, the responses of the two species when alarmed are basically different and, further, pink fry (Hoar, 1956) unlike chum fry retreat from bright light and go under stones prior to their first schooling. This latter difference was demonstrated in some unpublished experiments carried out at Port John Field Station of the Fisheries Research Board of Canada in 1956.

Pink and chum fry were compared prior to their first schooling. The method of obtaining such fish has been previously described (Hoar, 1956). Unschooled pink and chum salmon fry were kept individually in separate paper drinking cups (450 ml. capacity) from the time of capture (about midnight) until tested after 8 to 9 hours for their reaction of disappearing under stones when released. In comparable experiments 68.6% of 140 pink fry disappeared as compared to 19.4% of 144 chum fry.

At the present time it is impossible to decide whether the "surfacing" behaviour is absent in chum fry, masked by some other factors or less highly developed than in pink fry. It seems likely, however, that the differences demonstrated are of real significance in the early life history of the two species. Prior to the formation of large schools—presumably in the estuaries—the intensely schooling pink salmon fry may be at a disadvantage in small numbers and the behaviour of rising in darkness and retreating in the bright light will have real survival value. The chum fry, on the other hand, may find just as great a survival value in a less intense schooling reaction which permits a retreat as individuals under cover when in danger. In these as in several other respects (precise two-year cycle, strong sexual dimorphism) the pink salmon seems to be more specialized than the chum.

The sockeye salmon fry also showed a marked change in their responses to light between the first and second period of testing—about 10 weeks (Fig. 4). The recently emerged fry are relatively inactive in the depth preference tank, remaining near the bottom and characteristically retreating beneath the stones in the bottom of the tank. Of all the fish tested sockeye fry were the only ones which took cover among the stones at the bottom of the 180-cm. tank. The larger (Table I) and older fry move in larger numbers into the brighter (upper) areas and emerge from the cover of stones, swimming in the upper water of the 180-cm. tank (Fig. 4). In nature, marked differences in behaviour are observed which may be correlated with stage of development of this species. Whereas the recently emerged fish frequently pass down rivers and streams during the night (Hoar, 1954), an active upstream migration of (somewhat older?) fry has also been described (Int. Salmon Comm., 1949; Johnson, 1956). The differences in photoresponse observed here may have some significance in these movements.

The smolt transformation, in both coho and sockeye salmon, is associated with an increased sensitivity to light and a retreat to darker and deeper areas. The data recorded here are in accord with observations and experiments described elsewhere for these species. It is now appreciated that the behaviour of the sockeye salmon smolts in the 180-cm. tank (Fig. 4) should be interpreted as "escape behaviour" and does not reflect an indifference of these fish to light as at one time suggested (p. 92—Hoar, 1954). The cross-sectional area of this tank does not permit a fish of the size of sockeye smolt to form a school. The characteristic spreading of schooling fishes in a horizontal but not in a vertical plane has been noted by several writers (Keenleyside, 1955). Coho smolts, which do not school, apparently behave normally in the relatively narrow tank.

Although both sockeye and coho smolts prefer deeper and darker areas than

the fry of the same species, they frequently swim into the most intense of the experimental illuminations. In nature, both kinds of smolts are sometimes seen moving about in bright light during the day. During the period of downstream migration, sockeye as well as coho smolts may be seen in rivers and the sockeye smolts are commonly evident around the shores of lakes during this period. The mass exodus from the fresh water, however, takes place at night and these fish seem to be most active at low light intensity.

SUMMARY

1. The reactions of chum, pink, sockeye and coho salmon fry and coho and sockeye salmon smolts are compared at a series of different light intensities.

2. Schools of chum and pink salmon fry show a marked preference for light while sockeye fry retreat to darker areas. Coho fry are indifferent to light of moderately high intensities but become inactive at very low intensities.

3. Recently emerged pink salmon fry rise rapidly to the surface as the light intensity falls and retreat to deeper waters with increased illuminations. Chum fry do not seem to have this behaviour pattern. An attempt has been made to relate these differences to the intensity of the schooling behaviour and the alarm reactions of the two species.

4. Recently emerged sockeye retreat from bright light and take shelter under stones. Older sockeye fry rise into shallower water and brighter light but at no time show the strong light preference of the chum and pink salmon fry.

5. The smolt stage of both sockeye and coho salmon is associated with an increased sensitivity to light and a retreat to darker and deeper areas.

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Nematodes in the Fillets of Cod and other Fishes in Newfoundland and Neighbouring Areas[1]

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ABSTRACT

Inspection of the fillets of cod and other fish species for nematodes was carried out mainly in the years 1947 to 1953. Fillets were examined on a candling table. Two varieties of nematodes were found: one, 94% in cod and 86% of the total in American plaice, witch flounder, haddock and redfish, was *Porrocaecum*, ranging between 15–16 and 57–58 mm. in length; the other, 6% in cod and 14% of the total for the other 4 fish species mentioned above, did not possess a caecum and had a longer pharynx than *Porrocaecum* relative to the total length and to the ventriculus length. The latter nematode was 17–18 to 33–34 mm. in length and resembled *Anisakis* but may possibly have been *Eustoma*.

The infection level per 100 lb. (45 kg.) of cod fillets was lowest, 1 to 6 nematodes in ascending order, on Flemish Cap, the Grand Bank, the east coast of Newfoundland, off Labrador and southern St. Pierre Bank. It was highest, 223 nematodes, in the southern part of the Gulf of St. Lawrence. Intermediate values, 10 to 65 nematodes, were present in other areas. The nematode infection level in the larger American plaice was similar to that in cod, and infection per 100 lb. of fillets was especially heavy at the smaller sizes of plaice. Witch flounder, redfish and haddock showed low infection levels. Smelts living in the immediate neighbourhood of seal colonies were sometimes highly infected in terms of nematodes per 100 lb. of fillets. Nematodes were found in the fillets of the angler, Greenland cod, Greenland halibut, pollock, yellowtail flounder, longhorn sculpin and tomcod. It was concluded that the site of original infection of the fish was close to the site of deposition of nematode eggs by the seal host, and that the first intermediate hosts, invertebrates or small fish, were not very migratory.

In the fillet, nematodes were most numerous in the thicker parts dorsal and posterior to the body cavity and less numerous in the thinner tail portion. The distribution fits the idea that nematodes emerging from the stomach of the fish enter the neighbouring body muscles.

Of the seals which are the final hosts for *Porrocaecum*, harbour seals are common in Newfoundland areas where nematode infection of cod is high, as on the west coast of the island, but they are also especially numerous in southern Labrador where nematode infection of cod is low. The usual intermediate invertebrate or fish hosts may be scarce or lacking in Labrador and on the northeast coast of Newfoundland.

It is concluded that the larger, browner, and more numerous *Porrocaecum* presents the problem of commercial importance, rather than the smaller, whiter *Anisakis*. The only practical biological attack in view at the moment is the reduction in numbers of harbour and grey seals, in the hope that the more numerous harp seal is not so important a final host as it at first sight appears to be in the Gulf of St. Lawrence. In many areas where harp seals are not present, or, where present, do not carry *Porrocaecum*, the harbour and grey seals appear to be the only final hosts of *Porrocaecum*. St. Mary's Bay, Newfoundland, has many advantages as a site for a practical long-term experiment on reduction of nematode levels in cod flesh.

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INTRODUCTION

In most of the Gulf of St. Lawrence and in some other marine areas of eastern Canada, infection of the flesh of cod, *Gadus callarias* L., with nematodes presents a problem of considerable economic and scientific importance. During a survey of the incidence of nematode infection in the fishes of the eastern Canadian area, over 15,000 cod and lesser numbers of other fish species were examined. The survey was carried out chiefly between 1947 and 1953. The principal localities of the eastern Canadian area mentioned in the text are shown in Figures 1A and 1B.

The most common nematode in the somatic musculature of fishes of the Northwest Atlantic is *Porrocaecum decipiens* (Krabbe). Margolis (1956) reviews the relevant literature and accepts the view of Johnston and Mawson (1945) that species of this type, lacking interlabia, should be referred to the genus *Terranova* established by Leiper and Atkinson (1914) for *Terranova antarctica* from a New Zealand shark. Dollfus (1953) prefers *Porrocaecum* (*Terranova*) *decipiens*, and regards the *Terranova* type as sub-generic in status. In this paper, for convenience and because there is no agreement among recent writers regarding what, if any, change is desirable in the long-established generic name of this species, we shall refer to the genus as *Porrocaecum* and to the species as *Porrocaecum decipiens*.

MATERIALS AND METHODS

Fish in the ungutted condition, usually several days old and well iced, were brought to the St. John's Station of the Fisheries Research Board by the research vessel *Investigator II* from the various areas where the vessel had been fishing. Thus, almost all the samples from offshore areas as well as those from the inshore St. John's area were examined at the Station, while many of the remaining inshore samples were examined by Station personnel on shore, on long-lining vessels under contract to the Station, and on the *Investigator II*. Over half the cod and all of the other fishes were examined at the Station. The skinned fillets, only, were examined, and the nematodes were observed by candling over glass, using a 150-watt bulb at the Biological Station and a 100-watt bulb or occasionally

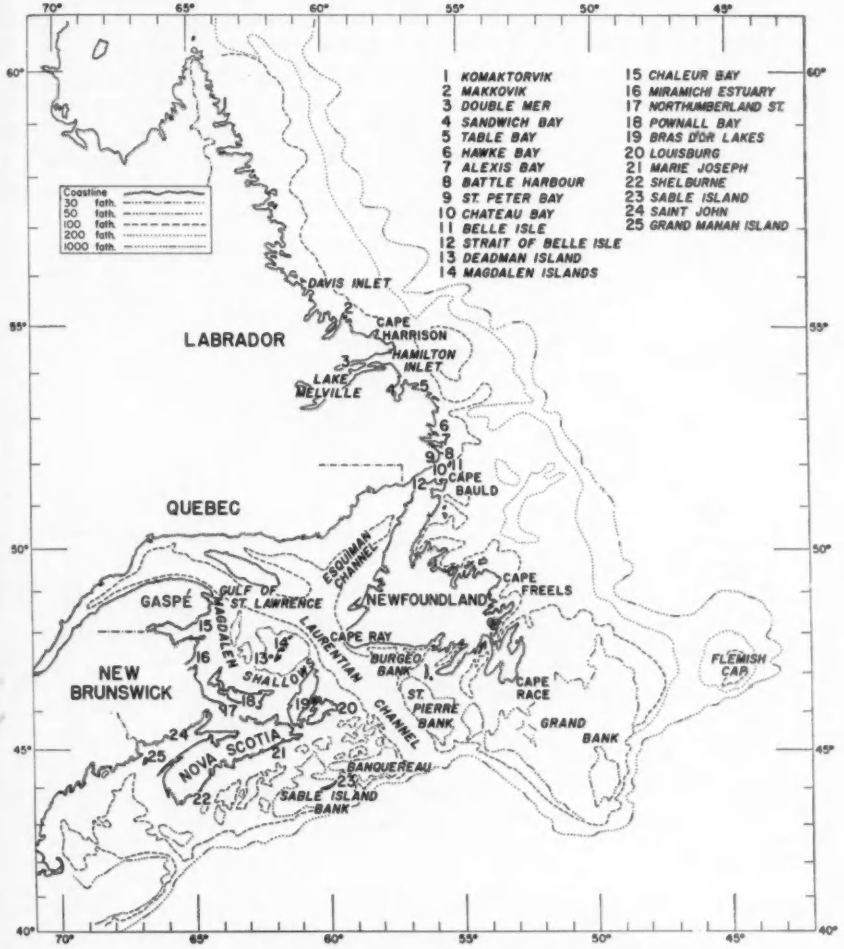

FIGURE 1A. Map showing principal localities of the eastern Canadian area mentioned in the text.

a high-powered flashlight in a dark room, in the field. All opaque areas, blood spots or other marks which might indicate nematodes were investigated. Usually all except the smaller fillets were sliced, either horizontally or vertically, into small strips for observation. It is believed that most of the nematodes present were recorded and the comparative data should be substantially reliable. Since there are nematodes, as a rule either *Anisakis* or *Contracaecum*, in the body cavity of many marine fishes, the fillets were dipped in fresh water before being candled, in order to remove any free nematodes from the surface of the fillets.

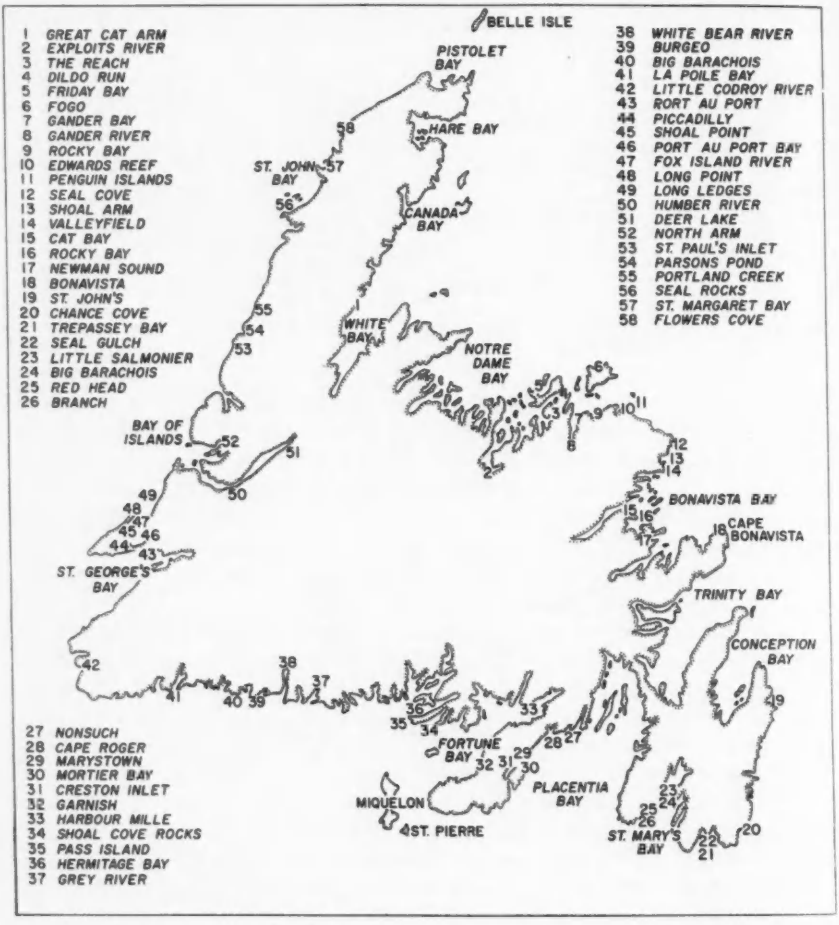

FIGURE 1B. Map showing principal Newfoundland localities mentioned in the text.

The length, sex, stage of maturity and usually the weight of the fish were recorded. The fish length used is the median length, from the most anteriorly projecting part of the head (either the snout or the tip of lower jaw depending on species) with the mouth closed, to the posterior mid-point of the caudal fin. The fish were measured on a centimetre measuring board with the first space measuring 1½ cm.

The weights used for cod are in most cases those of the individual fish, and in a few cases the weights were taken from a length-weight curve. For smelt the individual weights were taken from a length-weight curve. For other fishes the weights were obtained from length-weight curves and represent the weights

of fish at the mid-point of the length ranges used in the various tables. Where, however, at the beginning and end of a table, wide ranges are used, the weight data were first of all computed for the narrower length ranges and then combined.

At the Station the inspection was carried out by four biologists. In the field a considerable number of biologists and experienced technicians took part in the operation.

The outlines of the fishes in Figures 18 to 22 have been mainly copied from Bigelow and Schroeder (1953).

NEMATODE SPECIES IN FILLETS OF COD AND OTHER FISHES

Nematode Measurements

The total length, the length of the muscular pharynx (called pharynx length in remainder of discussion), the length of the ventriculus and, where present, the length of the caecum of the nematodes were measured as indicated in Figure 2.

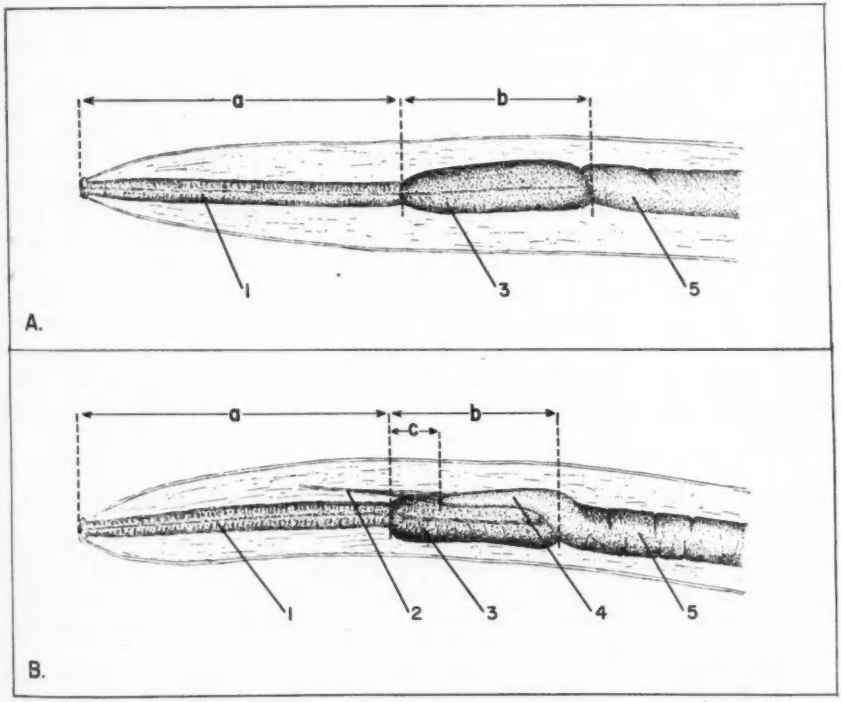

Figure 2. Nematode body proportions measured. Anterior region of A. *Anisakis*-type; B. *Porrocaecum*. *a*, total length of pharynx; *b*, total length of ventriculus; *c*, length from anterior end of ventriculus to anterior tip of caecum. 1, pharynx; 2, ligament; 3, ventriculus; 4, intestinal caecum; 5, intestine.

The nematodes, after preservation in 7% formalin, were straightened in a groove in a block of paraffin wax and measured to the nearest millimetre. Body proportions were measured by ocular micrometer, a conversion factor to millimetres being applied. The pharynx was not usually significantly curved; when slight curves were present they were straightened by use of dissecting needles. When the pharynx was very coiled or curved, measurement was not made, or 2 or 3 sectional measurements were made and totalled. The ventriculus was usually not too greatly curved for measurement. The length of that part of the ventriculus which was not covered by the caecum was measured, and this length was subtracted from the ventriculus total length to give the length of the caecum.

Lengths of Nematodes from Cod Fillets

Table I shows the length distributions of nematodes taken from the fillets of cod in various areas.[2] The lengths of the nematodes ranged from 13–14 mm. to 57–58 mm., and the average size was 36.9 mm. In areas of low nematode infection, such as the Grand Bank, the east coast of Newfoundland, and off Labrador, the average nematode size was considerably smaller than in areas, such as the Gulf of St. Lawrence, where nematode infection levels are high. In the areas of high incidence of infection (15 to 45%) only 3% of the nematodes were less than 25 mm., but in the areas of low infection (2 to 4%) 24% of the nematodes were below 25 mm. in length. Although, in general, there is evidence of only one mode, between 35 and 42 mm., in the nematode length frequencies from the areas of high infection, it is possible that in the areas of low infection, as indicated by Table I (total of A, B, C), there is a bi-modal length-frequency distribution, with one mode between 21 and 24 and a second between 33 and 40 mm. It is quite likely, however, that, with a greater number of measurements, this first mode would disappear, since, as will be noted in Table II, the increasing number of the larger *Porrocaecum* might compensate for the decreasing number of the smaller type which does not possess a caecum. There is, however, this indication from the length frequencies that more than one type of nematode may be present.

Lengths and Body Proportions of Nematodes, with and without Caeca, from Cod Fillets

All the nematodes present in the fillets possessed a pharynx and an oblong ventriculus of approximately the same shape. These nematodes either possessed *Porrocaecum*-type caeca or had no caeca, and for convenience in discussion we

[2]These length distributions are unselected except for the following 94 nematodes sent to Dr. D. M. Scott, March 1950: Grand Bank and Flemish Cap (A), 5 *Porrocaecum* and 3 below 20 mm. without caeca; Labrador (B), 7 *Porrocaecum*; east coast of Newfoundland (C), 19 *Porrocaecum* and 4 below 20 mm. without caeca; St. Pierre Bank (D), 9 *Porrocaecum* and 2 below 20 mm. without caeca; south coast of Newfoundland (G), 21 *Porrocaecum* and 2 below 20 mm. without caeca; west coast of Newfoundland (H), 19 *Porrocaecum* and 3 below 20 mm. without caeca.

TABLE I. Frequencies of total lengths of nematodes from the fillets of cod from various Newfoundland and neighbouring areas—A to I. (These are unselected samples apart from 94 nematodes—see text.)

A—Grand Bank and Flemish Cap
B—Labrador offshore and inshore
C—East coast Newfoundland
D—St. Pierre Bank
E—Nova Scotia banks
F—North Gulf of St. Lawrence
G—South coast Newfoundland
H—West coast Newfoundland
I—South Gulf of St. Lawrence

Total length of nematodes	Numbers of cod nematodes in fillets									Total A,B,C,	Total D,E,F, G,H,I	Total all areas
	A	B	C	D	E	F	G	H	I			
mm.												
13–14	1	...	...	...	...	...	2	...	...	1	2	3
15–16	...	...	...	...	1	...	1	...	...	...	2	2
17–18	5	...	1	...	1	...	...	...	1	6	2	8
19–20	4	1	1	1	...	...	5	1	...	6	7	13
21–22	4	4	4	3	1	3	11	2	2	12	22	34
23–24	3	4	4	2	2	2	6	5	4	11	21	32
25–26	1	2	3	7	1	5	7	7	9	6	36	42
27–28	7	...	...	5	2	4	12	15	14	7	52	59
29–30	5	1	6	6	8	2	35	26	24	12	101	113
31–32	5	3	3	9	9	6	52	32	40	11	148	159
33–34	7	1	9	12	14	1	50	46	77	17	200	217
35–36	5	5	6	15	19	7	64	43	84	16	232	248
37–38	3	3	6	7	19	5	90	40	77	12	238	250
39–40	4	4	8	15	13	11	74	33	68	16	214	230
41–42	4	3	5	11	15	8	63	40	89	12	226	238
43–44	1	1	3	12	6	6	42	27	59	5	152	157
45–46	1	...	...	2	5	2	38	26	50	1	123	124
47–48	...	...	...	1	1	2	20	13	34	...	71	71
49–50	...	...	...	1	...	2	6	5	13	...	27	27
51–52	...	...	...	...	1	...	1	2	13	...	17	17
53–54	...	...	...	...	...	1	1	...	...	...	2	2
57–58	...	...	...	...	...	...	...	1	...	...	1	1
Total nematodes	60	32	59	109	118	67	580	364	658	151	1,896	2,047
Average size, *mm.*	29.9	32.0	33.2	35.4	36.3	36.3	37.0	37.0	38.5	31.6	37.4	36.9
Standard deviation	7.92	7.53	6.89	6.48	5.82	7.62	6.31	6.25	5.93	7.54	6.26	6.53
Standard error	1.02	1.33	0.90	0.62	0.54	0.93	0.26	0.33	0.23	0.61	0.14	0.15
Percentage infected	2.2	3.6	3.7	15.0	15.7	19.2	19.9	29.5	45.1			

TABLE II. Numbers and body proportions of *Porrocaecum* and of nematodes without caeca, from cod fillets. (Linear measurements of body, pharynx and ventriculus.)

Total length of nematodes	Number of nematodes				Pharynx as percentage of body length		Ventriculus as percentage of body length		Pharynx as percentage of ventriculus		Caecum as percentage of body length in *Porrocaecum*	Caecum as percentage of ventriculus
	Porrocaecum	Without caeca	Total	Percentage without caeca	*Porrocaecum*	Without caeca	*Porrocaecum*	Without caeca	*Porrocaecum*	Without caeca		
mm.				%	%	%	%	%	%	%	%	%
15–16	1	...	1	...	8.1	...	5.6	...	145	...	3.7	66.7
17–18	2	2	4	50	8.8	9.4	5.3	5.0	167	189	2.4	44.4
19–20	3	2	5	40	6.8	10.5	4.7	4.4	145	210	1.6	33.3
21–22	1	7	8	88	7.7	8.7	3.6	4.2	213	211	2.3	62.5
23–24	5	11	16	69	7.2	8.4	4.7	4.3	154	201	2.6	55.6
25–26	9	11	20	55	6.5	8.7	4.1	4.3	157	200	2.2	52.3
27–28	9	17	26	65	6.7	8.0	3.9	3.9	169	208	2.6	65.6
29–30	29	7	36	19	6.0	7.4	4.0	3.9	151	192	2.3	57.4
31–32	55	3	58	5	5.8	7.6	3.8	3.4	153	218	2.2	58.3
33–34	97	4	101	4	5.9	6.7	3.5	3.4	163	194	2.3	62.5
35–36	120	...	120	0	5.7	...	3.7	...	154	...	2.3	61.5
37–38	155	...	155	0	5.4	...	3.5	...	154	...	2.0	57.4
39–40	134	...	134	0	5.3	...	3.3	...	162	...	2.0	61.5
41–42	120	...	120	0	5.1	...	3.2	...	162	...	2.0	61.5
43–44	97	...	97	0	5.0	...	3.1	...	159	...	2.0	63.2
45–46	84	...	84	0	5.0	...	3.0	...	161	...	2.0	64.3
47–48	49	...	49	0	4.7	...	3.2	...	150	...	2.1	66.7
49–50	25	...	25	0	4.9	...	3.2	...	153	...	2.1	65.6
51–52	16	...	16	0	4.5	...	2.8	...	159	...	1.9	65.9
53–54	1	...	1	0	4.5	...	2.6	...	171	...	0.9	35.7
55–56	...	...	...	...	...	...	...	...	...	...	...	...
57–58	1	...	1	0	4.3	...	2.6	...	167	...	1.7	66.7
Total	1,013	64	1,077	6								

shall for the present refer to the latter as being *Anisakis* (Baylis, 1920). Not one of 1,587 identified nematodes from cod fillets, nor of 124 identified nematodes from the fillets of other fishes, was of the *Contracaecum* type. *Porrocaecum*, often large and brownish, was usually in a very loose coil. *Anisakis* was usually tightly coiled in a spiral with several coils as in a small coil of rope, and was very often enclosed in a cyst. *Contracaecum*, often found by us in the body cavity or immediately below the peritoneum of the body wall of many fish species, including cod, capelin and redfish, was not found in the fillets. It usually was fairly straight, curved, or hooked as in a walking-stick, or, when occasionally coiled, only loosely coiled in not more than a coil or two.

Nematodes identified as *Porrocaecum* ranged in length from 15–16 to 57–58 mm., with the greatest number between 35–36 and 41–42 mm., while the length range of *Anisakis* was 17–18 to 33–34 mm., with the greatest number between 23–24 and 27–29 mm.

The lengths of the pharynx and the ventriculus, both in *Porrocaecum* and in the nematodes with caeca, decrease considerably relative to the total length of the nematode as the latter increases in length (Fig. 3, Table II).

The length of the ventriculus relative to the total length is approximately the same in *Porrocaecum* and in the nematodes without caeca (Table II). Also, in each of these varieties of nematode, pharynx and ventriculus maintain an approximately constant length-relationship to each other with increase in nematode length (Fig. 4). In *Porrocaecum*, however, the pharynx is shorter in relation to both total length of the nematode and ventriculus length (Fig. 3, 4, Table II) than in the nematodes without caeca.

The caecum in *Porrocaecum*, although showing considerable individual range in relative length at all nematode sizes, was on the average greatest, relative to the total length, at the smaller sizes (Fig. 5 and Table II). However, with increase in *Porrocaecum* length, the caecum grew faster than the ventriculus (Table II).

Lengths of Nematodes, with and without Caeca, from Fillets of Fishes other than Cod

Only 60 nematodes were measured from fishes other than cod (Table III). There was a higher percentage of small nematodes present than in the nematodes from cod fillets and the proportion of nematodes without caeca was correspondingly higher. Except for the lack of the larger specimens of *Porrocaecum*, both types of nematodes found in the fishes other than cod had approximately the same size range as the nematodes from cod fillets.

Nematode Infection in the Fillets of Cod and Other Fishes

Cod 41 cm. and over in Total Length

Figures 6 to 11 and Table IV indicate the location and size of samples and the degree of infection of cod with nematodes, as determined from the presence of nematodes in their fillets. In Table IV and Figure 11 the nematode infection rates have been summarized for natural areas and numbered in order (1 to 21) of increasing number of nematodes per 100 lb. (45 kg.) of fillets.

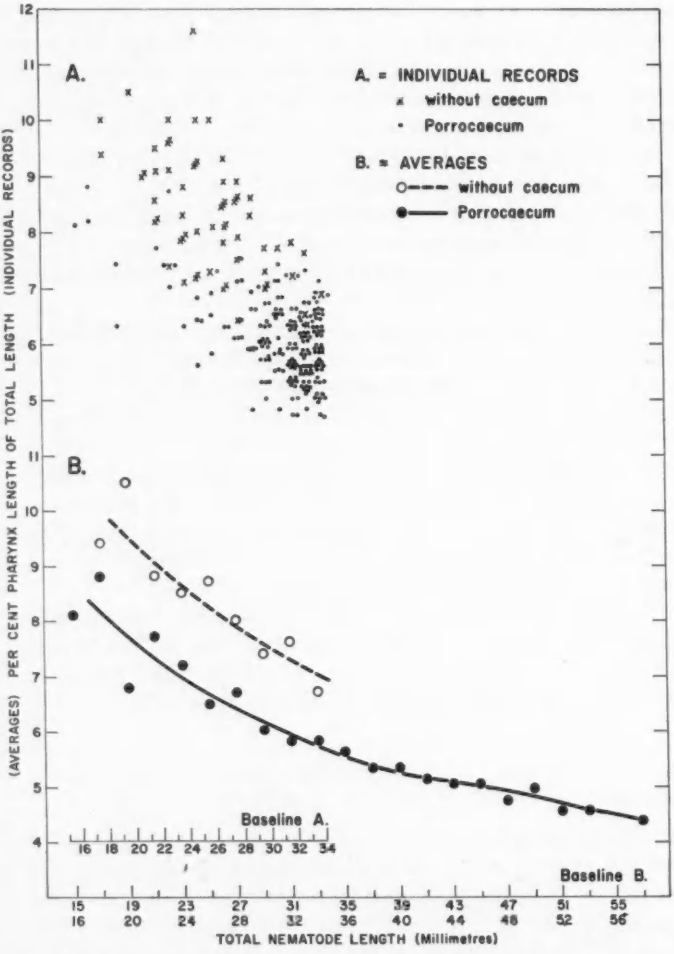

FIGURE 3. Pharynx length relative to the total length in *Porrocaecum* and in nematodes without caeca. (Because of their large numbers and the lack of nematodes without caeca, the individual records have not been given for *Porrocaecum* above 34 cm.)

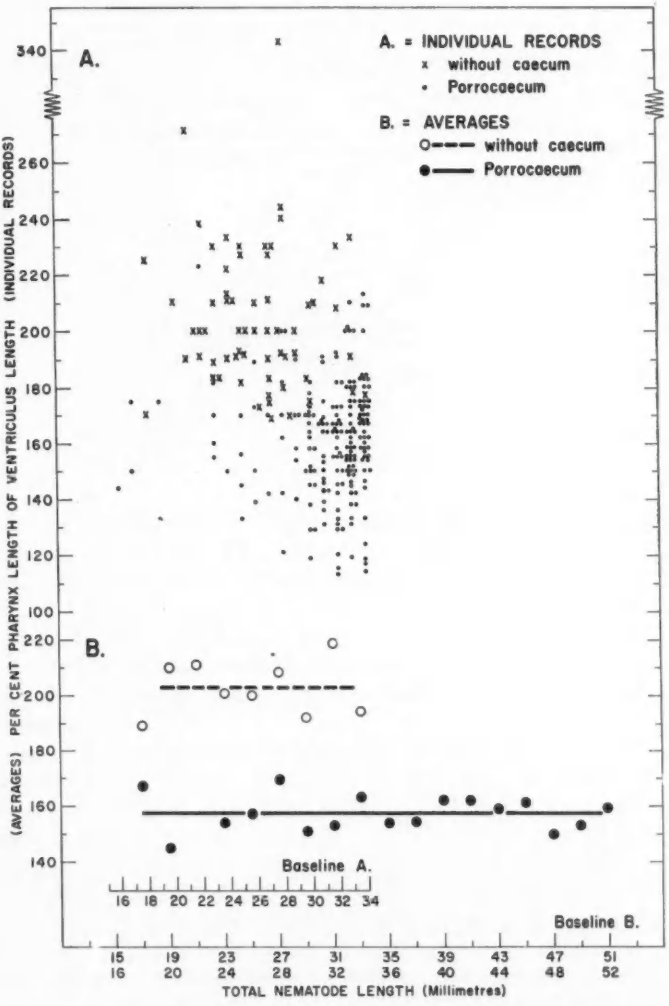

FIGURE 4. Pharynx length relative to ventriculus length in *Porrocaecum* and in nematodes without caeca. (Because of their large numbers and the lack of nematodes without caeca, the individual records have not been given for *Porrocaecum* above 34 cm. Averages of less than 2 individuals have been omitted.)

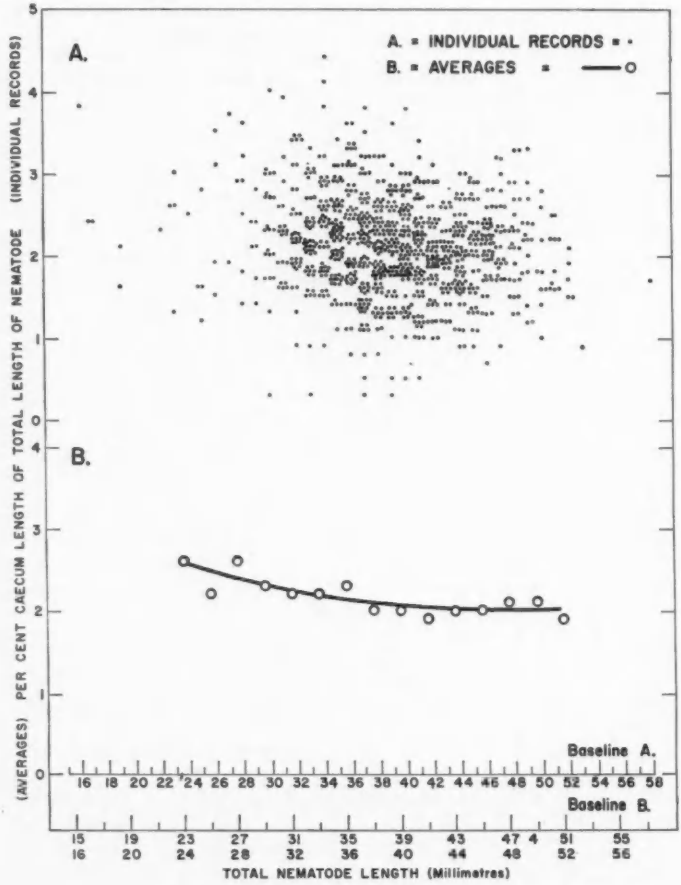

FIGURE 5. Relative length of the caecum to the total length in *Porrocaecum*.

TABLE III. Length frequencies of *Porrocaecum* and of nematodes without caeca, from fillets of fishes other than cod. (These fishes are as follows, with the number of nematodes of the *Porrocaecum* type and the number without caecum following in order: Greenland cod 1, 0; haddock 2, 2; pollock 0, 1; redfish 5, 2; American plaice 27, 1; witch flounder 3, 3; yellowtail flounder 1, 0; longhorn sculpin 2, 0; sea raven 1, 0; angler 1, 0; smelt, 8, 0.)

Nematode length range	No. of *Porrocaecum*	No. of nematodes without caeca	Total
mm.			
16–18	1	0	1
19–22	2	2	4
23–26	6	2	8
27–30	9	3	12
31–32	1	0	1
33–34	8	2	10
35–36	8	...	8
37–38	5	...	5
39–40	0	...	0
41–42	2	...	2
43–44	7	...	7
45–46	1	...	1
47–48	1	...	1
Total	51	9	60

The rate of infection of cod with nematodes (Fig. 8) is highest in the southern part of the Gulf of St. Lawrence, 53 to 80%, and on the west coast of Newfoundland, 21 to 49%. It is fairly high on the south coast of Newfoundland, 9 to 29%; on the northern part of St. Pierre Bank, 14 to 29%; and on the northern Nova Scotia banks, 3 to 23%, or, apart from one small sample, 9 to 23%. Infection is low on the Grand Bank, Flemish Cap, the east coast of Newfoundland, and off Labrador. Usually in these areas the infection rate is 0 to 3%, occasionally 4 to 6%, and in one rectangle 7%.

In terms of the number of nematodes in the fillets of 100 cod and the number of nematodes per 100 lb. of cod fillets (Fig. 9, 10), the differences described above are accentuated. Where the level of infection is low usually only one nematode is present per infected fish, but there may be many nematodes per infected fish in areas of high infection. For example, the southern part of the Gulf of St. Lawrence shows 208 to 465 nematodes per 100 cod and 142 to 322 nematodes per 100 lb. of fillets. High infection levels are shown by the cod of the southern half of the west coast of Newfoundland, 90 to 113 nematodes per 100 cod, and 39 to 75 nematodes per 100 lb. of fillets; and also by the cod of the northern St. Pierre Bank area including St. Pierre and Miquelon, and from Burgeo Bank landward along the western part of the south coast of Newfoundland, 45 to 128 nematodes per 100 cod, and 26 to 91 nematodes per 100 lb. of fillets. On the northern Nova Scotia banks and the northern half of the west coast of Newfoundland nematode incidence is lower, and it is somewhat lower still on the eastern section of the south coast of Newfoundland. Nematode infection is lowest on the Grand Bank, Flemish Cap, the east coast of Newfoundland,

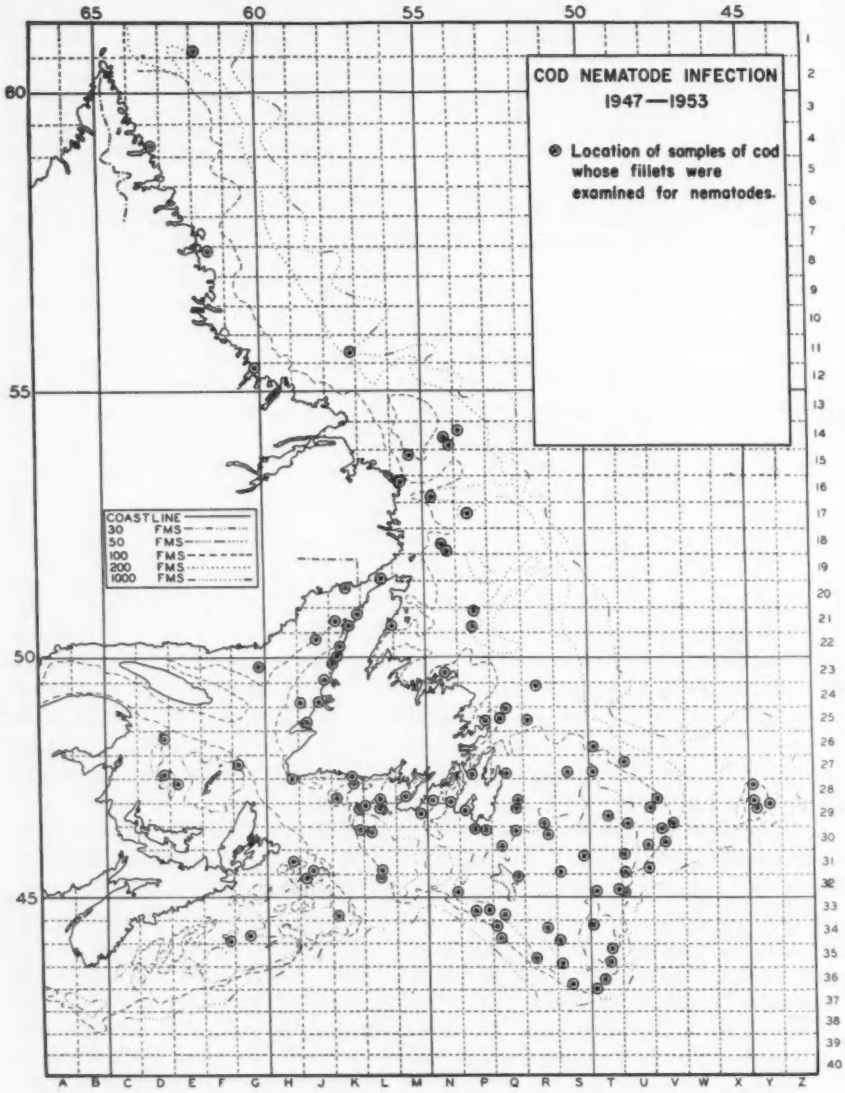
COD NEMATODE INFECTION
1947—1953
Location of samples of cod whose fillets were examined for nematodes.
COASTLINE
30 FMS
50 FMS
100 FMS
200 FMS
1000 FMS
65
60
55
50
45
80
55
50
45
A B C D E F G H J K L M N P Q R S T U V W X Y Z
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40

FIGURE 6. Location of random samples of cod whose fillets were examined for nematodes.

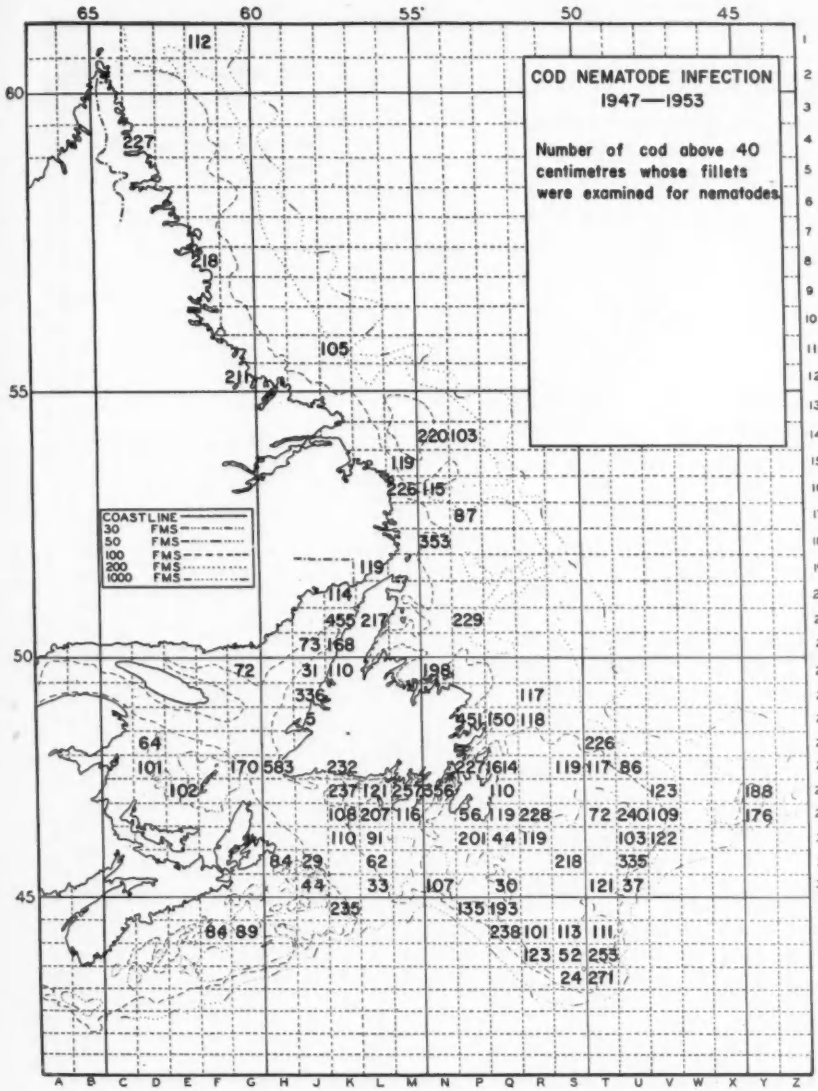

FIGURE 7. Number of cod, 41 cm. and over, whose fillets were examined for nematodes; data summarized for rectangles of one degree longitude by a half-degree latitude.

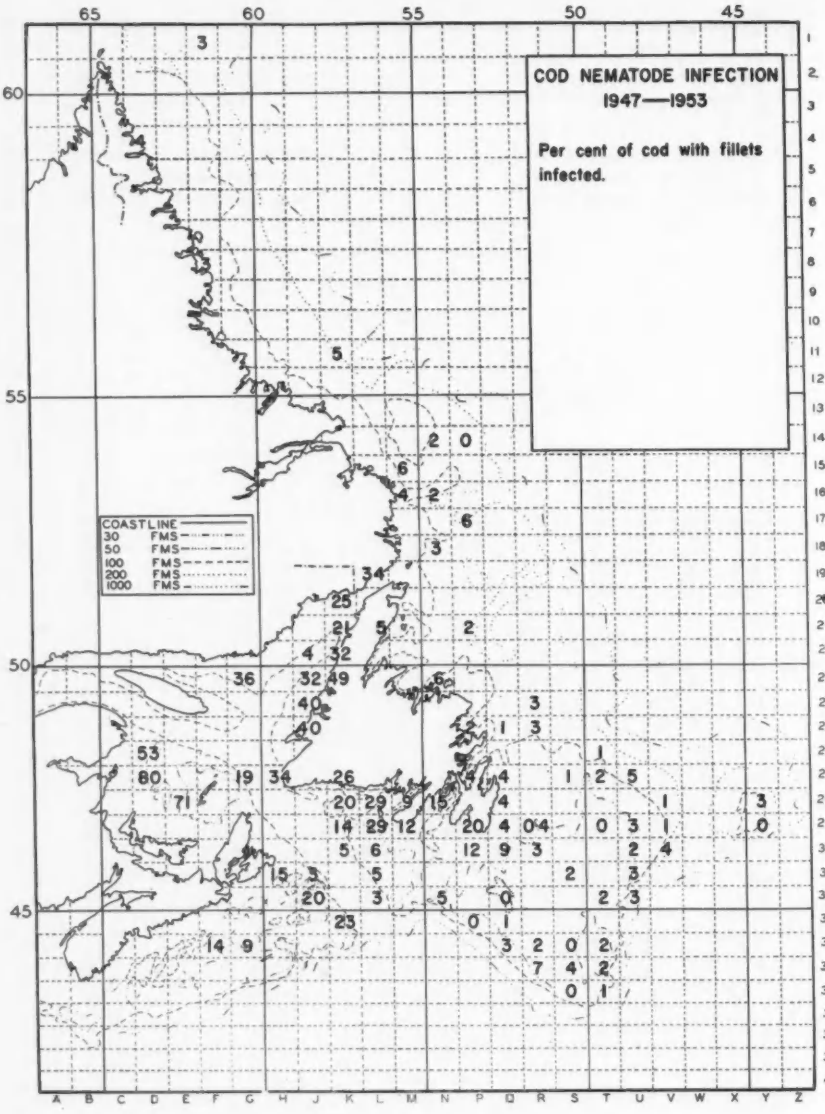

FIGURE 8. Percentage of cod, 41 cm. and over, with fillets infected with nematodes; data summarized for rectangles of one degree longitude by a half-degree latitude.

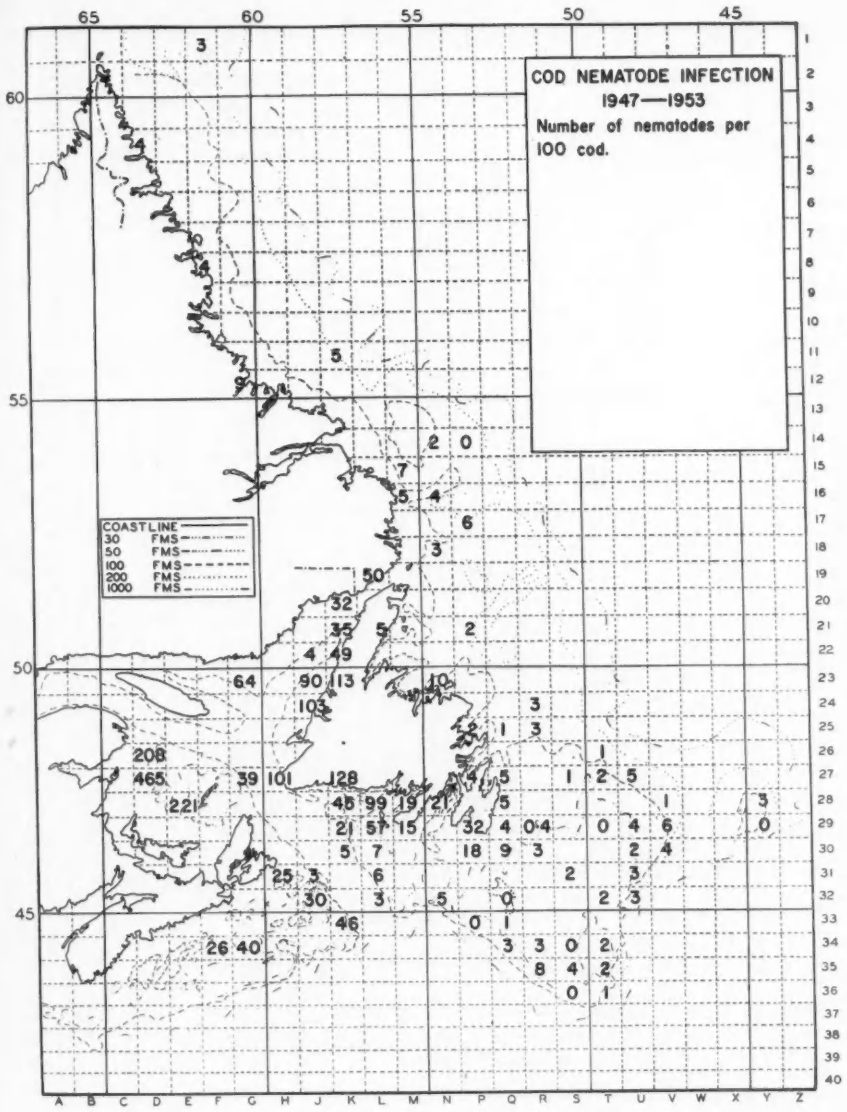

FIGURE 9. Number of nematodes in fillets of 100 cod 41 cm. and over; data summarized for rectangles of one degree longitude by a half-degree latitude.

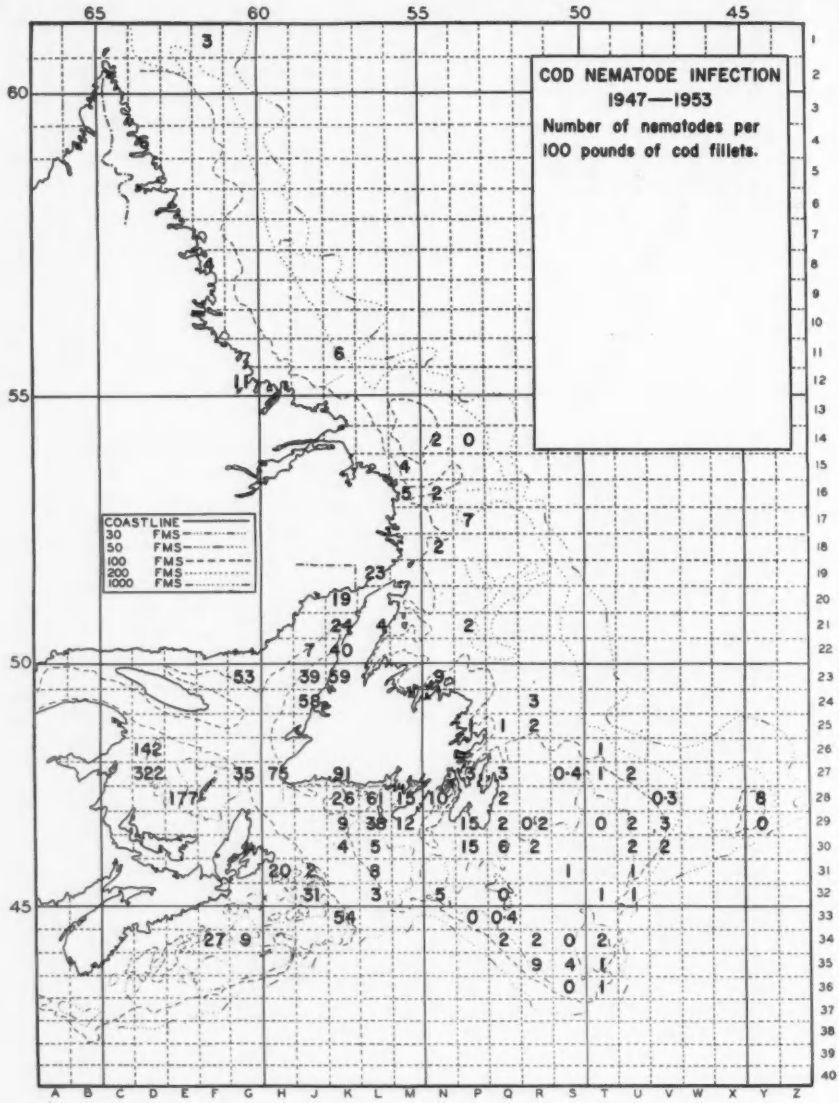

FIGURE 10. Number of nematodes in 100 lb. (45 kg.) of cod fillets; data summarized for rectangles of one degree longitude by a half-degree latitude (All the cod were 41 cm. and over in length.)

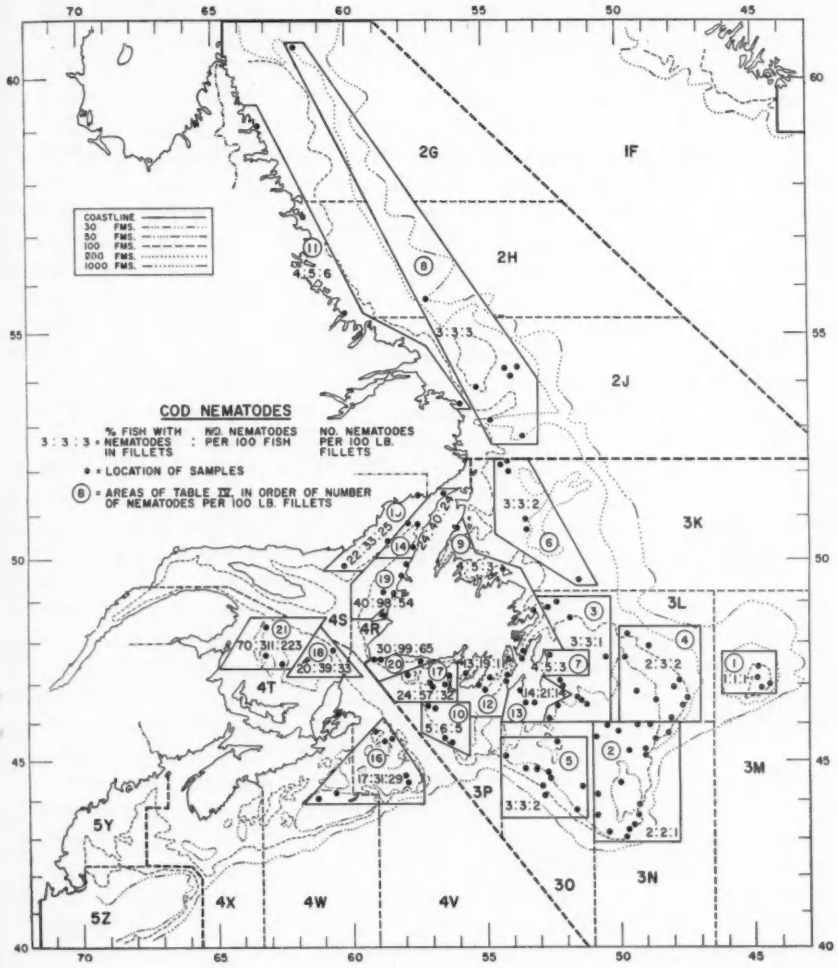

FIGURE 11. Infection of cod with nematodes, 1947 to 1953, as determined by examination of the fillets: summary of infection rates by area; for reference numbers to areas and other data see Table IV. (All the cod were 41 cm. and over in length.)

TABLE IV. Nematode infection in cod of commercial size, 41 cm. and over, as determined by destructive examination of the fillets.

Reference No.	Locality and ICNAF subdivision	No. cod	Gutted weight	Percentage of cod with nematodes in fillets	No. of nematodes per 100 cod	No. of nematodes per 100 lb. of fillets	No. of nematodes identified	Percentage *Porrocaecum*	Percentage *Anisakis*
			lb.	%				%	%
1	Flemish Cap: 3M	357	1,517	1.4	1.4	1.0	3	0	100
2	SE. Grand Bank: 3N	1,550	8,717	1.9	1.9	1.0	7	43	57
3	N. Grand Bank: 3L[1] W. of long. 50° W.	1,004	6,397	2.5	2.6	1.2	8	75	25
4	N. Grand Bank: 3L[2] E. of long. 50° W.	1,196	6,529	2.2	2.7	1.5	16	75	25
5	SW. Grand Bank: 3O	922	4,036	2.5	2.8	1.9	14	29	71
6	NE. coast Nfld.—offshore: 3K	699	2,990	3.0	3.0	2.1	3	67	33
7	St. John's: 3L[1]	1,611	7,232	3.7	4.7	3.1	31	84	16
8	Labrador—offshore: 2G, 2H, 2J	851	2,760	3.1	3.4	3.2	11	36	64
9	E. coast Nfld. inshore: 3K, 3L[1]	1,089	4,545	3.8	4.6	3.3	14	100	0
10	St. Pierre Bank south of lat. 46°30′ N.: 3P	344	1,159	4.9	5.8	5.2	16	94	6
11	Labrador—inshore: 2G, 2H, 2J	880	2,191	4.3	5.1	6.2	16	94	6
12	S. coast Nfld.—Cape St. Mary's to Pass Island: 3P	736	3,863	12.5	18.9	10.8	97	97	3
13	Cape Race to Cape St. Mary's: 3L[1]	257	1,152	14.0	21.4	14.3	7	57	43
14	N. section of Nfld. W. Coast—N. of Portland Creek: 4R	629	3,079	23.9	39.8	24.4	105	92	8
15	N. Gulf of St. Lawrence: 4S	259	1,013	22.4	32.8	25.2	50	84	16
16	Nova Scotia banks: 4V, 4W	553	1,789	17.0	31.1	28.9	101	98	2
17	St. Pierre Bank north of lat. 46°30′ N. and Burgeo Bank: 3P	551	2,923	24.3	57.0	32.2	109	92	8
18	S. Gulf of St. Lawrence (deeper water, 51–90 fath.): 4T	169	595	19.5	39.1	33.3	28	100	0
19	S. section of Nfld. W. coast—S. of Portland Creek: 4R	599	3,288	39.7	98.1	53.6	190	96	4
20	S. coast Nfld.—Pass Island to Cape Ray: 3P	935	4,260	30.4	99.1	65.3	362	97	3
21	S. Gulf of St. Lawrence—(shallow water, 26–50 fath.): 4T	267	1,113	70.0	310.5	223.2	399	100	0
Total		15,458	71,148	10.5	24.5	16.0	1,587	94.3	5.7

off Labrador, and on the southern part of St. Pierre Bank, with usually 0 to 3 and more rarely 4 to 10 nematodes per 100 cod and generally 0 to 3 and occasionally 4 to 9 nematodes per 100 lb. of fillets. On the Grand Bank and Flemish Cap the nematode infection rate is lower than in any of the other areas.

All nematodes in the cod fillets from the southern part of the Gulf of St. Lawrence were *Porrocaecum*. Of those from the remainder of the Gulf, the Nova Scotia banks, the south coast of Newfoundland as far east as Placentia Bay, and St. Pierre Bank, between 92 and 98% were *Porrocaecum*, except from the north shore of the Gulf where 84% were *Porrocaecum*; the remaining nematodes were *Anisakis*. Thus, in all areas both inshore and offshore which had heavily infected cod, almost all the nematodes were *Porrocaecum*. Similarly, in the inshore areas of the Newfoundland east coast and Labrador almost all the nematodes from cod fillets, 84–100%, were *Porrocaecum* (Fig. 12 and Table IV).

The only exception to the above is the high percentage of *Anisakis* (43%) in area 13 (St. Mary's Bay and off Trepassey Bay). This area has harbour seal colonies which should provide *Porrocaecum* eggs; also, from unpublished results of cod tagging, the area is known to receive many cod immigrants from the southwestern part of the Grand Bank where, in the fillets of cod, *Anisakis* is more abundant than *Porrocaecum*. Only a few nematodes (7), however, were examined and these were not from St. Mary's Bay but from a cod sample taken about 10 nautical miles off Cape Pine.

Much higher proportions of *Anisakis* were present in the offshore areas of eastern Newfoundland and Labrador and on the Grand Bank and Flemish Cap, but few nematodes were examined. On the northern half of the Grand Bank, 25%; on the southern half of the Grand Bank, 57 to 71%; on the Flemish Cap, of the 3 nematodes examined, 100%; and in offshore Labrador, 64% of the nematodes examined were *Anisakis*; the remainer were *Porrocaecum*.

From the commercial viewpoint, therefore, the great difference between centres of high nematode infection (such as the Gulf of St. Lawrence) and offshore centres of very low infection (such as the southern Grand Bank), shown in Figure 11, are slightly accentuated. While almost all the nematodes in the centres of high infection (and also in the inshore areas of low infection) are *Porrocaecum*, over half the nematodes from the southern half of the Grand Bank and Flemish Cap areas are the smaller *Anisakis* which are less visible to the consumer than the larger and darker *Porrocaecum*.

American Plaice, *Hippoglossoides platessoides* (Fabricius)

The area showing the highest infection levels for American plaice (Fig. 13) were the southern Gulf of St. Lawrence and the west coast of Newfoundland, with 21 and 10% respectively of the plaice infected. The northern part of the St. Pierre Bank-Fortune Bay area had 4% infection, the northern Nova Scotia banks 2%, Labrador and the northeast Newfoundland area (ICNAF Subdivision 3K) each had 1% of the plaice infected. The Grand Bank, with 0.2% of the plaice infected in Subdivision 3L and 3N, and 0% infected in Subdivision 3O; and Flemish Cap (3M), with 0% infected, possessed the lowest levels of infection. High and low levels

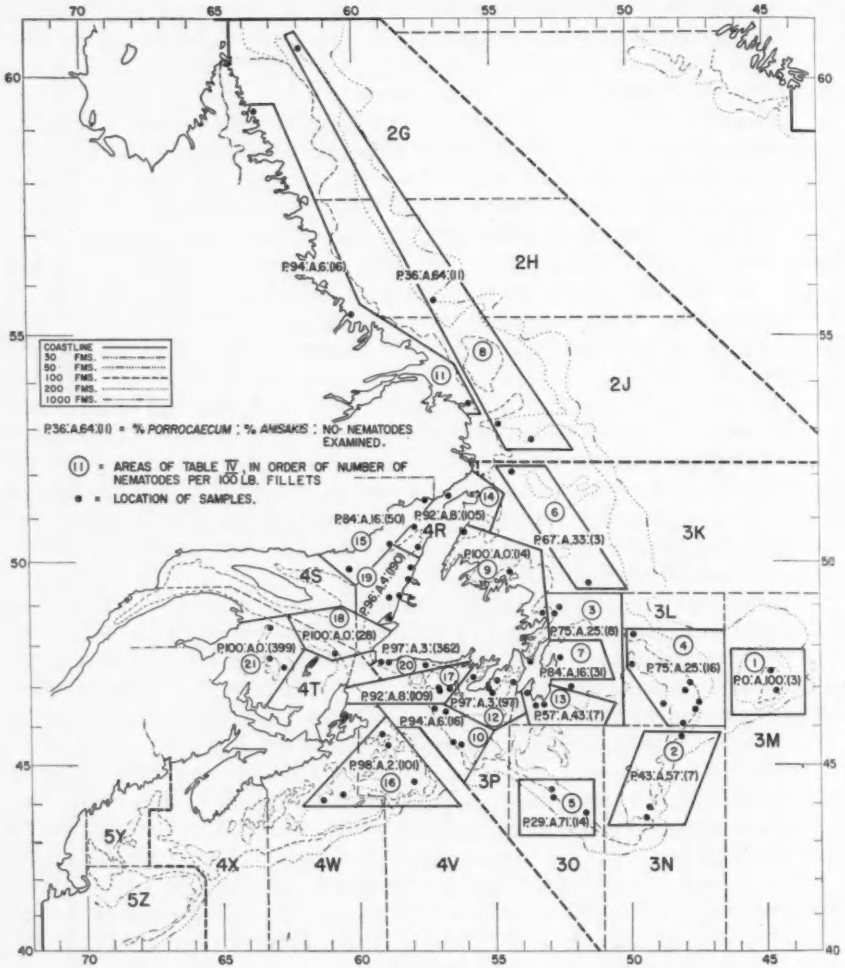

FIGURE 12. Infection of cod fillets with nematodes, 1947 to 1953: percentage *Porrocaecum* and percentage of *Anisakis*. For reference numbers to areas and other data see Table IV.

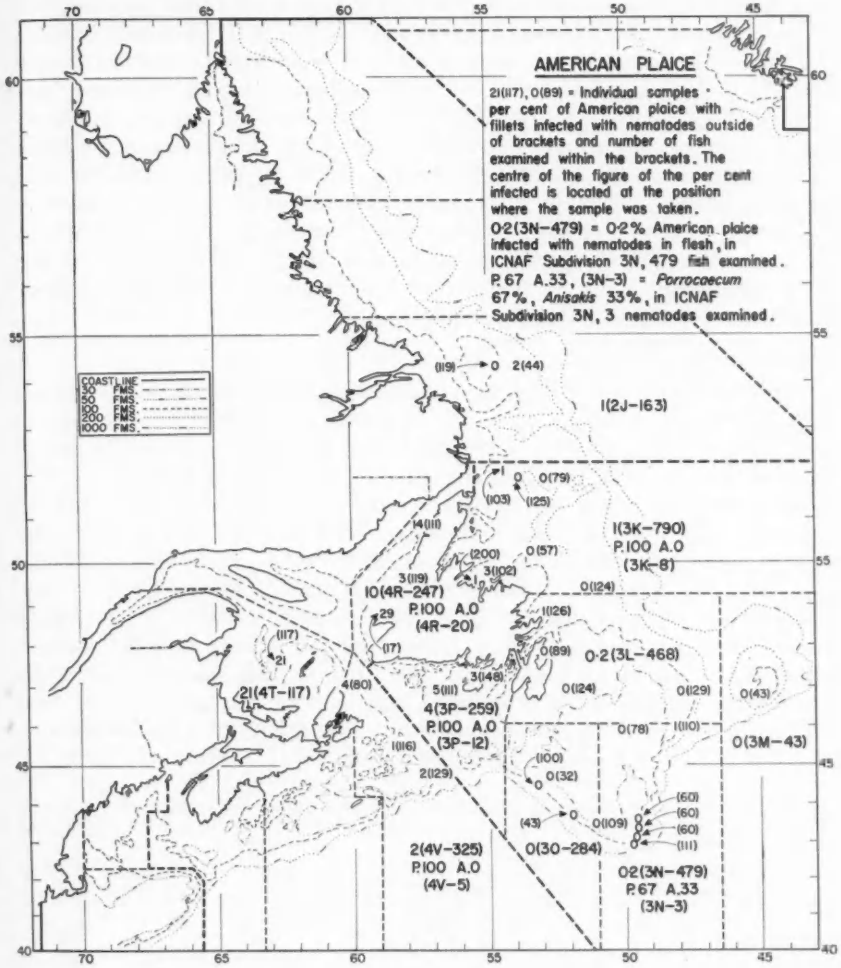

FIGURE 13. Infection of American plaice with nematodes, 1949 to 1953: percentage of plaice with fillets infected; percentage of *Porrocaecum* and percentage of *Anisakis* in plaice fillets. Data for nematode infection of plaice samples from individual locations, and also summarized for ICNAF subdivisions.

of nematode infection in the plaice occur in the same areas which have high and low levels respectively in the cod (Fig. 7 to 11). Although the nematode infection levels shown in Figure 13 for the American plaice are considerably less than in cod, it must be remembered that in considering the plaice all sizes have been used, while for the cod only individuals of commercial size (41 cm. and over) were considered. As indicated in Table IX, the degree of infecton of the larger American plaice approaches that of the cod, especially when considered from the point of view which has the most commercial importance–the number of nematodes per 100 lb. of fillets. Plaice smaller than the 31 to 40 cm. group are non-commercial and, in the Newfoundland area, usually the lower half of this group, also, would be discarded. Of 48 nematodes examined from American plaice fillets, 98% were *Porrocaecum* and 2% *Anisakis* (Fig. 13, Table V).

WITCH FLOUNDER, *Glyptocephalus cynoglossus* (L.)

Although the levels of nematode infection of witch flounder (Fig. 14) are lower than those of American plaice, the patterns of areas of infection are approximately similar. There are some small differences which may be due to the lack of adequate material, or more likely are because the plaice, particularly the very young specimens, on the average, live in and were obtained from somewhat shallower water than the witch. Nematode infection levels of the witch, like those of the plaice, were highest in the southern Gulf of St. Lawrence, 6%, and from the Sable Island Bank (Subdivision 4W), 4%. The lowest infection rates, 0%, were found off the northeast coast of Newfoundland and the northern half of the Grand Bank area (3L). On St. Pierre Bank and the south coast of Newfoundland (3P) and southern Grand Bank (3O) areas, the infection levels were slightly higher, 1%. An unexpected zero infection rate off the west coast is based on only 17 witch and is probably not significant. Of 9 nematodes from witch flounder fillets, 6 were *Porrocaecum* and 3 *Anisakis* (Fig. 14 and Table V).

TABLE V. Total nematodes identified, and percentages of *Porrocaecum* and percentages of *Anisakis* in American plaice, witch flounder, haddock and redfish fillets, in various ICNAF subdivisions (3K, etc.) 1949–1956.

Fish species	3K	3N+3O	3P	4R+4S +4T	4V+4W	Total
	A. Total nematodes					
American plaice	8	3	12	20	5	48
Witch flounder	...	1	2	3	3	9
Haddock	...	1	...	1	2	4
Redfish	...	...	8	6	8	22
Total	8	5	22	30	18	83
	B. Percentage *Porrocaecum*					
American plaice	100	67	100	100	100	98
Witch flounder	...	0	100	100	33	67
Haddock	...	0	...	100	100	75
Redfish	...	...	63	50	88	68
Total	100	40	86	90	83	86
	C. Percentage *Anisakis*					
American plaice	0	33	0	0	0	2
Witch flounder	...	100	0	0	67	33
Haddock	...	100	...	0	0	25
Redfish	...	...	38	50	13	32
Total	0	60	14	10	17	14

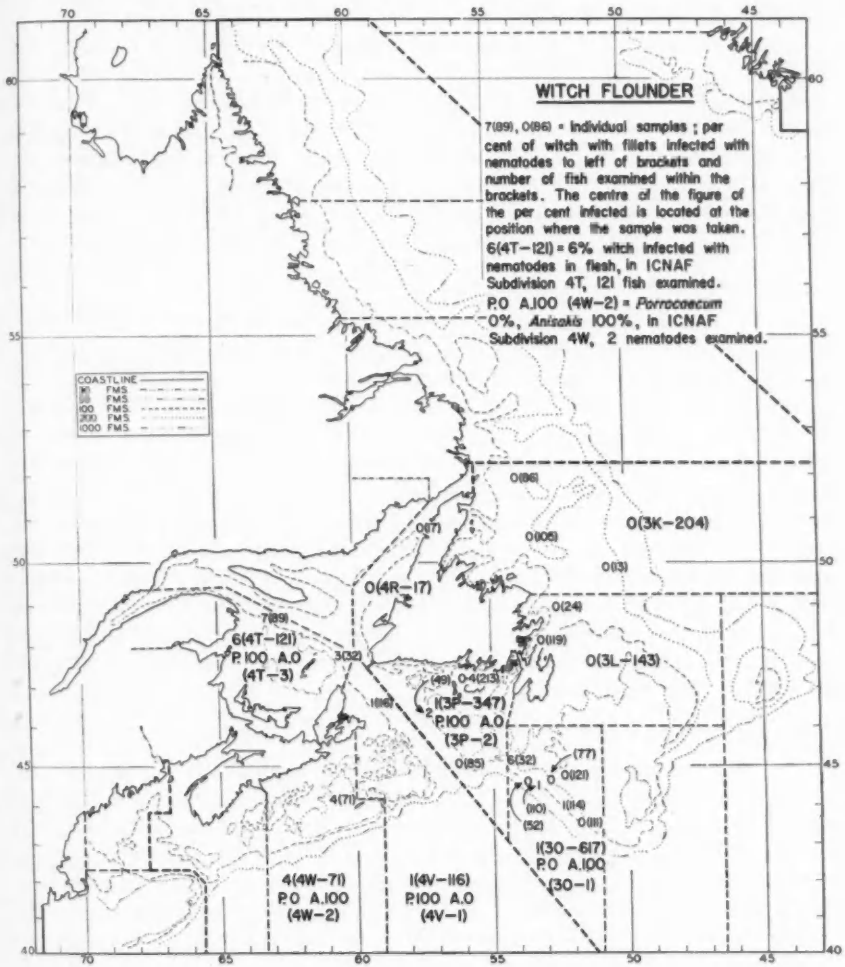

FIGURE 14. Infection of witch flounder with nematodes, 1949 to 1953: percentage of witch with fillets infected; percentage of *Porrocaecum* and percentage of *Anisakis* in witch fillets. Data for nematode infection of witch samples from individual locations, and also summarized for ICNAF subdivisions.

HADDOCK, *Melanogrammus aeglefinus* (L.)

Haddock have a lower incidence of nematode infection than the plaice or witch flounder (Fig. 15). The infection rate was highest, 2%, for the west coast of Newfoundland (4R) and for each of the two northern subdivisions of the Nova Scotia banks (4V and 4W). A very low infection rate, 0.4%, was found in Grand Bank haddock from Subdivision 3O. No nematode infection was noted in the fillets of large samples of haddock from St. Pierre Bank and vicinity (3P) and from the north and southwest Grand Bank (3L, 3N). Of 4 nematodes from haddock fillets, 3 were *Porrocaecum* and 1 *Anisakis* (Fig. 15 and Table V).

REDFISH, *Sebastes marinus* (L.)

In the redfish the incidence of nematode infection in the fillets is low (Fig. 16), approximately similar to that of the haddock. The infection rate was highest, 8%, in a small sample of redfish from the northern end of the deep water Esquiman Channel off the west coast of Newfoundland. The average infection rate was about 2% along the southern side of the deep Laurentian Channel from Gaspé to the northeast corner of Banquereau (4T and 4V). There was, however, no infection in 3 samples from the western slope of St. Pierre Bank (3P), forming the northeastern border of the Laurentian Channel. No nematode infection was found in redfish from the Grand Bank and Flemish Cap (3L, 3N and 3M), off northeast Newfoundland (3K), nor, with the exception of 0.2% in 2J, off Labrador. Most of the modestly high infection rates were close to shore near areas where the cod were highly infected. Distant from the shore there was usually little or no infection. Of 22 nematodes from redfish fillets, 68% were *Porrocaecum* and 32% *Anisakis* (Fig. 16, Table V).

SMELT, *Osmerus mordax* (Mitchill)

In smelt, instead of fillets, "sides" were examined, that is, halves of the body wall with the gut, head, skin and vertebral column removed. On the east coast of Newfoundland the infection rate of smelt by nematodes was moderately low (Fig. 17), only slightly higher than that for cod (Fig. 8). However, in terms of infection per 100 lb. of smelt sides, the infection rate was very much higher than that for cod fillets of the same general area: 54 to 88 for smelt compared with 3 nematodes per 100 lb. of cod fillets (Fig. 11). In Placentia Bay (Creston Inlet in Mortier Bay) the infection rate for smelt was very similar to that for cod, but the number of nematodes per 100 lb. of fillets was very much greater, 352 for smelt and 11 for cod. (This difference would be considerably larger if smelt fillets instead of sides had been examined.) No infection was evident in smelt of the Little Codroy area and very low individual infection rates were found in the smelt of Fortune Bay (Garnish) and Port au Port Bay (Piccadilly Brook), despite the fact that these areas are near highly infected cod populations. In the Port au Port Bay area, however, the infection rate per 100 lb. of smelt sides is of the same order as that of the cod per 100 lb. of fillets. In relation to seal colonies (Fig. 23) the smelt rivers or brooks, from which the moderately infected Friday Bay and Valleyfield samples were obtained, are near but not in the

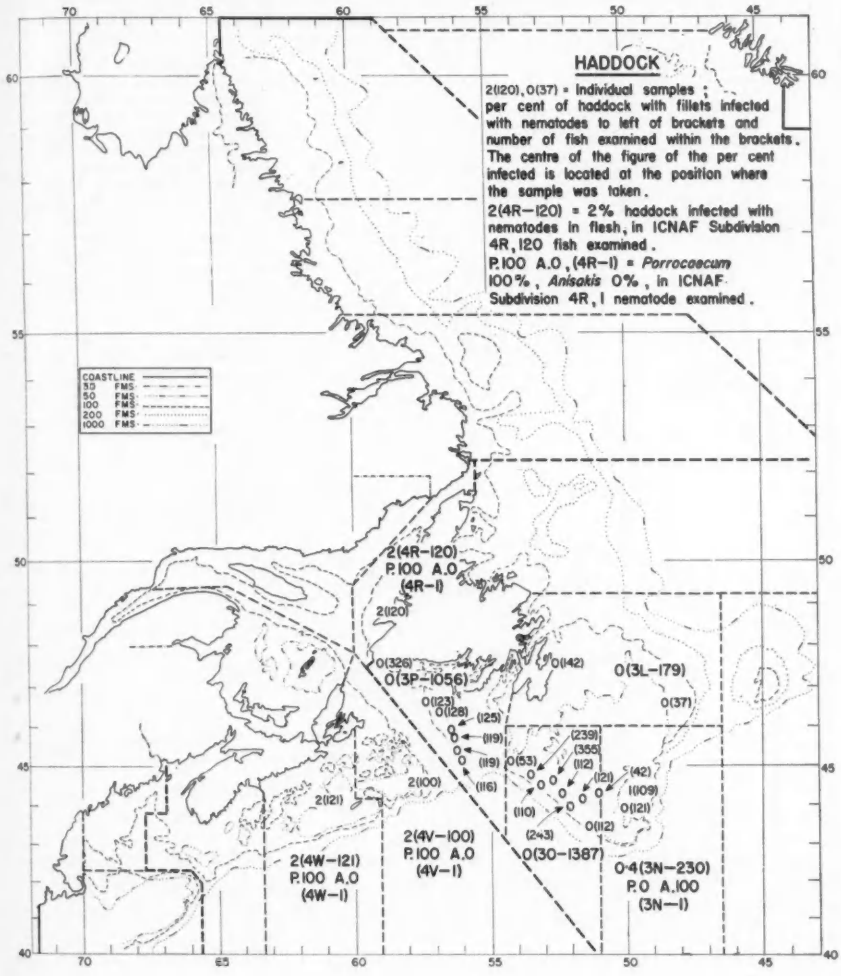

FIGURE 15. Infection of haddock with nematodes, 1949 to 1953: percentage of haddock with fillets infected; percentage of *Porrocaecum* and percentage of *Anisakis* in haddock fillets. Data for nematode infection of haddock samples from individual locations, and also summarized by ICNAF subdivisions.

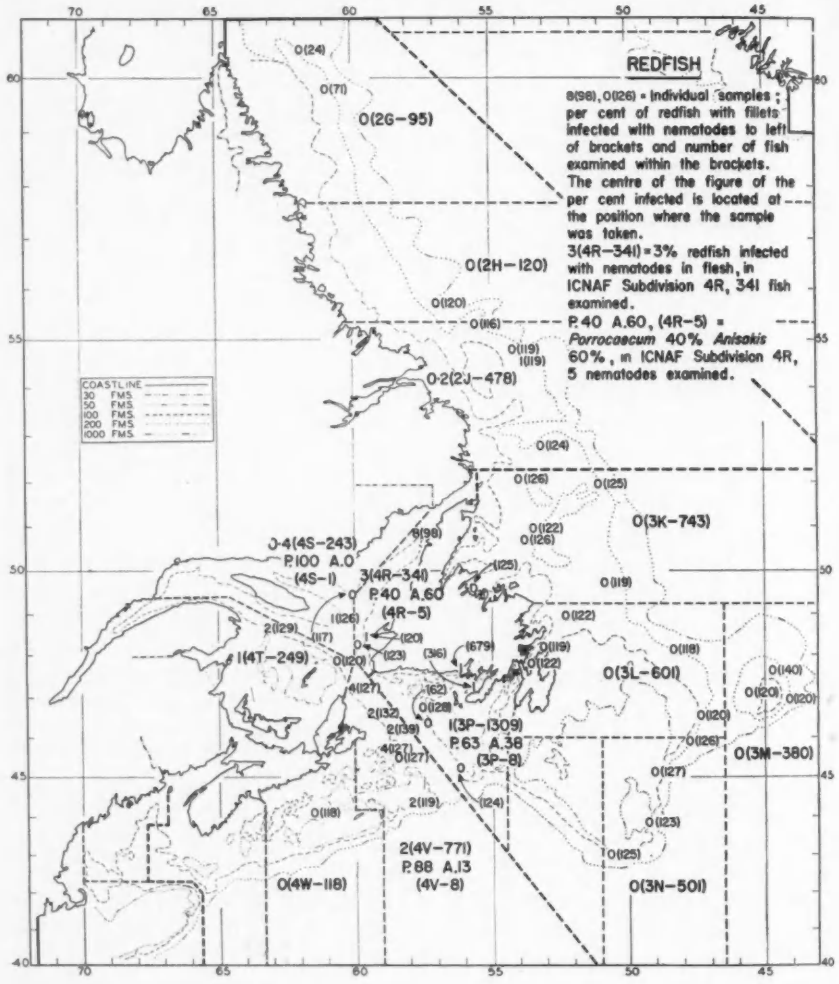

FIGURE 16. Infection of redfish with nematodes, 1949 to 1956: percentage of redfish with fillets infected; percentage of *Porrocaecum* and percentage of *Anisakis* in redfish fillets. Data for nematode infection of redfish samples from individual locations, and also summarized for ICNAF subdivisions.

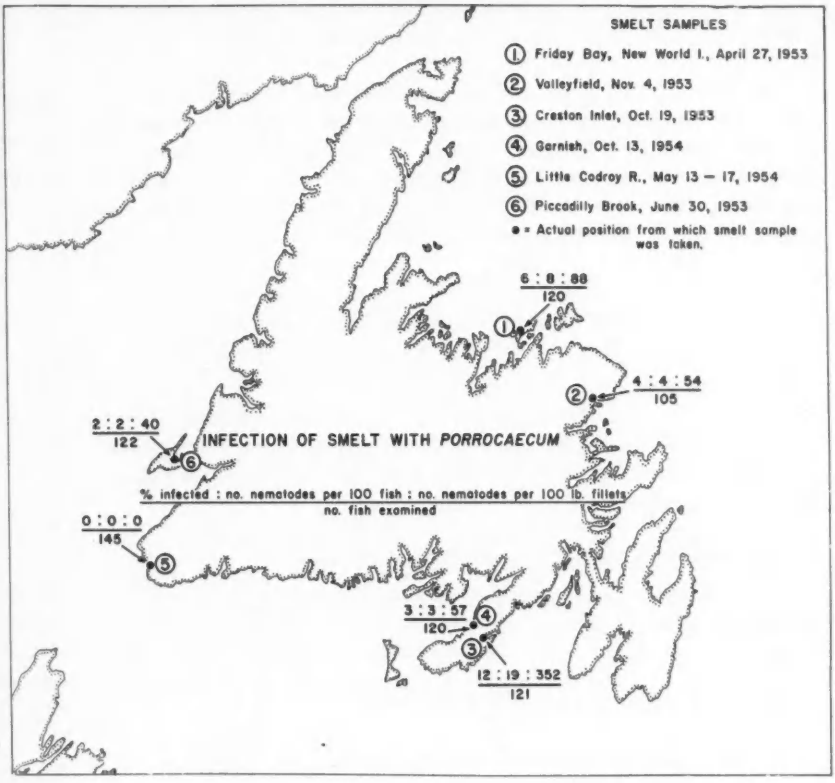
SMELT SAMPLES
① Friday Bay, New World I., April 27, 1953
② Valleyfield, Nov. 4, 1953
③ Creston Inlet, Oct. 19, 1953
④ Garnish, Oct. 13, 1954
⑤ Little Codroy R., May 13 — 17, 1954
⑥ Piccadilly Brook, June 30, 1953
● = Actual position from which smelt sample was taken.
INFECTION OF SMELT WITH PORROCAECUM
% infected : no. nematodes per 100 fish : no. nematodes per 100 lb. fillets
no. fish examined
6 : 8 : 88
120
4 : 4 : 54
105
2 : 2 : 40
122
0 : 0 : 0
145
3 : 3 : 57
120
12 : 19 : 352
121

FIGURE 17. Infection of smelt with *Porrocaecum*, 1953 to 1954.

immediate vicinity of seal colonies. In the most highly infected area, Creston Inlet in Mortier Bay, the smelt area and the feeding grounds of the harbour seal colony are the same. All of 22 nematodes, identified from the sides of the smelt, were *Porrocaecum*.

OTHER FISHES

Of 18 nematodes identified from the fillets of other fishes, only 1 nematode from pollock, *Pollachius virens* L., was *Anisakis*, the remaining 17 were *Porrocaecum*. The fish from which the nematodes were obtained for examination and the number of nematodes identified (in parentheses) were: pollock, (1); Greenland cod, *Gadus ogac* Richardson, (1); yellowtail flounder, *Limanda ferruginea* (Storer), (1); longhorn sculpin, *Myoxocephalus octodecimspinosus* (Mitchill), (3); the sea raven, *Hemitripterus americanus* (Gmelin), (10); the angler, *Lophius americanus* Cuvier and Valenciennes, (1); and the tomcod, *Microgadus tomcod* (Walbaum), (1).

RELATIVE NEMATODE INFECTION IN THE FILLETS OF MALE AND FEMALE COD

In Table VI the data on nematode infection of cod in several size ranges have been combined in groups of increasing percentage infection. These extensive data show that no very obvious or large differences exist in nematode infection of male and female cod either in the same size range or in the over-all population. Consequently, it is possible and more convenient to consider data on nematode infection of cod without reference to the sex of the host.

RELATION OF THE DEGREE OF NEMATODE INFECTION IN THE FILLETS TO THE LENGTH OF THE FISH

Cod

Tables VII and VIII show the relation of cod nematode infection to the total length of the cod in 12 areas from the northern Nova Scotia banks to Labrador. The data from these areas have been arranged in the order of the number of nematodes per 100 lb. of fillets.

PERCENTAGE OF COD WITH NEMATODES IN FILLETS

Areas 1 and 2 in which infection is low (2 to 4%), show no increase in the percentages of cod infected beyond the 31 to 50 cm. range. In the remaining areas, all except area 3 (4%) with higher infection rates (12 to 66%), infection increases with increase in cod size in all except area 8, which shows a decrease in infection at the largest sizes.

NUMBER OF NEMATODES IN FILLETS OF 100 COD

The general picture here is the same as that for the percentage of cod infected, but there is generally a greater increase in the number of nematodes present from the smaller to the larger fish sizes. Low infection areas 1 and 2 again show no increase in infection with increasing length of fish. Area 8 (northern Nova Scotia banks) shows a considerable decrease in infection at the largest sizes. The increase in the number of nematodes per 100 cod does not generally keep pace with the increasing weight of the fish.

NUMBER OF NEMATODES PER 100 LB. OF COD FILLETS

In the areas of low infection (1 and 2), from which by far the greatest amounts of cod are obtained, and also in area 8, there is a rapid decrease, with increasing fish size, in the number of nematodes per 100 lb. of fillets. Areas 3, 4 and 10 also show a decrease in nematode infection with increasing fish size. In areas 5, 6 and 12 there is at first an increase in nematode infection per 100 lb. of fillets, followed by a decrease at the largest sizes. Areas 7 and 11 show an increase and then a levelling off in nematode infection with increasing size. In area 9 a slight decrease is followed by a large increase, but the large increase is based on only 13 fish. This is, in any case, a group of fish from deep water on

TABLE VI. Comparative rates of nematode infection in male (M) and female (F) cod.

1. Grand Bank: 3N, 3O; 3K offshore; 3L offshore; Flemish Cap
2. Nfld. east coast, inshore
3. Labrador, inshore and offshore
4. Nfld. south coast: Cape Race to Pass Island
5. St. Pierre Bank: 3P
6. North shore Gulf of St. Lawrence: 4S
7. West coast Nfld.: 4R north of Portland Creek
8. Nova Scotia banks: 4V and 4W
9. Southern Gulf of St. Lawrence: 4T (deeper water, 51 to 90 fath.)
10. West coast Nfld., south of Portland Creek: 4R
11. South coast Nfld., inshore: Pass Island to Cape Ray
12. Southern Gulf: 4T (shallow water, 26 to 50 fath.)

Locality	Length range of cod	Total fish			Gutted weight			Percentage of fish with nematodes		No. of nematodes per 100 fish		No. of nematodes per 100 lb. of fillets		No. of nematodes per infected fish	
		M	F	F	M	F	F	M	F	M	F	M	F	M	F
	cm.			%	*lb.*	*lb.*	%	%	%						
1–3	31–50	1,168	1,170	50	1,759	1,767	50	2.4	3.1	3.3	4.1	6.7	8.2	1.4	1.3
4–5	,,	298	314	51	334	434	57	4.4	8.3	4.4	8.9	11.7	19.4	1.0	1.1
6–9	,,	277	237	46	395	325	45	10.1	11.8	14.1	13.5	29.7	29.5	1.4	1.1
10–11	,,	172	191	53	272	294	52	22.1	19.4	27.9	33.5	52.9	65.5	1.3	1.7
12	,,	55	40	42	69	49	42	40.0	52.5	67.4	87.6	161.3	226.0	1.7	1.7
1–3	51–70	2,644	3,084	54	9,458	11,346	55	3.0	3.2	3.6	3.4	3.0	2.8	1.2	1.1
4–5	,,	440	421	49	1,604	1,532	49	13.6	15.9	23.9	32.5	19.7	26.8	1.8	2.0
6–9	,,	482	491	51	1,843	1,736	49	20.1	20.2	35.7	33.6	28.0	28.5	1.8	1.7
10–11	,,	429	524	55	1,565	1,915	55	32.7	30.9	88.6	74.8	72.9	61.4	2.7	2.4
12	,,	93	85	48	346	316	48	74.3	69.4	338.9	266.2	273.0	214.8	4.6	3.8
1–3	71–150	1,152	1,407	55	9,934	13,049	57	2.2	2.6	2.3	3.3	0.8	1.1	1.1	1.2
4–5	,,	260	241	48	2,437	2,345	49	20.0	19.5	40.8	39.4	13.1	12.1	2.1	2.0
6–9	,,	140	142	50	1,081	1,283	54	33.5	33.8	60.0	65.5	23.3	21.8	1.8	1.9
10–11	,,	164	242	60	1,565	2,377	60	42.1	42.6	156.1	178.8	49.1	54.8	3.7	4.2
12	,,	18	24	57	161	219	58	89.0	87.5	616.7	579.2	207.2	190.8	6.9	6.6
Total	31–50	1,970	1,952	50	2,829	2,869	50	6.6	7.6	8.9	10.6	18.7	21.8	1.4	1.4
,,	51–70	4,088	4,605	53	14,816	16,845	53	10.9	10.5	26.1	22.3	21.6	18.2	2.4	2.1
,,	71–150	1,734	2,056	54	15,178	19,273	56	12.1	12.5	33.7	39.2	11.6	12.5	2.8	3.1
Over-all total	31–150	7,792	8,613	52	32,823	38,987	54	10.1	10.3	23.4	23.7	16.7	15.7	2.3	2.3

TABLE VII. Numbers of cod and gutted weights of cod used for calculating rates of nematode infection in Table VIII. For identification of the localities (1, 2, etc.) see Table VI.

Length range	Locality 1	2	3	4	5	6	7	8	9	10	11	12
cm.	A. TOTAL COD											
21–30	95	...	...	42	5	8	...	40	9	93	2	...
31–50	1,163	578	597	313	299	131	76	226	81	170	193	95
51–70	2,917	1,647	1,164	490	371	131	376	350	116	301	652	178
71–150	1,935	556	68	309	192	48	180	41	13	166	240	42
	B. TOTAL GUTTED WEIGHT OF COD IN TABLE A, ABOVE, IN LB.											
21–30	31	...	...	11	2	3	...	12	3	24	0.4	...
31–50	1,710	921	896	408	431	171	125	334	90	254	312	117
51–70	11,178	6,049	3,578	1,807	1,329	480	1,352	1,129	419	1,067	2,384	662
71–150	17,530	4,888	565	2,898	1,885	405	1,458	379	121	1,843	2,099	379
Total A	6,110	2,781	1,829	1,154	867	318	632	657	219	730	1,087	315
,, B	30,449	11,858	5,039	5,124	3,647	1,059	2,935	1,854	633	3,188	4,795	1,158

TABLE VIII. Rates of infection of cod (of Table VII) with nematodes and average weights of individual cod in the various size ranges. (In the range 21 to 30 cm. where numbers of cod examined are few, an asterisk indicates samples where fish numbers were so low that the nematode infection has not been considered in the discussion. Skinless fillets have been estimated as one-third of the gutted, head-on weight.)

Length range	Locality 1	2	3	4	5	6	7	8	9	10	11	12
cm.												
	A. PERCENTAGE OF COD WITH NEMATODES IN FILLETS											
21–30	0	...	...	5	20*	13*	...	8	0*	12	0*	...
31–50	2	4	3	6	6	8	8	15	9	26	16	45
51–70	3	4	4	13	17	27	20	18	20	39	29	72
71–150	2	3	7	17	24	31	38	10	54	49	38	88
	B. NUMBER OF NEMATODES IN FILLETS OF 100 COD											
21–30	0	...	...	7	180*	13*	...	8	0*	26	0*	...
31–50	2	8	3	7	7	9	8	20	9	39	23	75
51–70	3	5	4	17	42	41	32	36	30	94	75	304
71–150	2	3	12	31	55	44	68	12	215	145	187	595
	C. TOTAL NEMATODES PER 100 LB. OF COD FILLETS											
31–50	4	14	6	15	14	21	14	41	23	79	43	185
51–70	2	4	4	14	35	34	27	34	17	80	61	245
71–150	1	1	4	10	17	16	25	4	69	39	64	198
	D. NUMBER OF NEMATODES PER INFECTED FISH											
31–50	1.0	1.8	1.2	1.1	1.1	1.2	1.0	1.4	1.0	1.5	1.5	1.7
51–70	1.0	1.3	1.1	1.3	2.5	1.5	1.6	2.0	1.5	2.4	2.6	4.2
71–150	1.2	1.0	1.6	1.8	2.3	1.4	1.8	1.3	4.0	3.0	4.9	6.8
	E. AVERAGE WEIGHTS OF THE COD IN THE VARIOUS SAMPLES, IN LB.											
31–50	1.5	1.6	1.5	1.3	1.4	1.3	1.6	1.5	1.1	1.5	1.6	1.2
51–70	3.8	3.7	3.1	3.7	3.6	3.7	3.6	3.2	3.6	3.5	3.7	3.7
71–150	9.1	8.8	8.3	9.4	9.8	8.4	8.1	9.2	9.3	11.1	8.7	9.0
	AVERAGES OF TOTALS, 31–150 CM.											
A	2	4	4	12	15	19	24	16	18	38	28	66
B	2	5	4	18	33	28	40	29	33	93	90	274
C	1	3	4	12	23	25	26	29	35	56	62	224
D	1.1	1.3	1.2	1.5	2.2	1.5	1.7	1.8	1.9	2.5	3.2	4.1
E	5.0	4.3	2.8	4.6	4.2	3.4	4.6	3.0	3.0	5.0	4.4	3.7

the southern slope of the Laurentian Channel, which had a very much lower infection rate than fish from the adjacent shallow water area of the Magdalen Shallows (12) in the same ICNAF subdivision (Table VIII). From the results of tagging experiments (McKenzie, 1956) it can be assumed that the cod of this region migrate enough to render it likely that the larger fish could in part be fish which obtained a large supply of nematodes in the shallower parts of Subdivision 4T, while the smaller fish are much more likely to be resident cod.

NUMBER OF NEMATODES IN FILLETS PER INFECTED COD

In general, nematode incidence in fillets of infected cod increases with size of fish, but there is no evidence of this in one of the three areas of low infection (2) and only slight indication of significant increase in the area of lowest infection (1). In area 8 there is a decrease in infection at the larger sizes but this is based on a small number of cod.

American Plaice

Our most extensive data on nematodes in plaice fillets (Table IX) are from the Grand Bank and from east Newfoundland and Labrador areas. In these areas nematode infection is low and shows no very definite trend at increasing sizes in percentage of fish infected. Of the remaining four areas where the infection rate is higher, only one ICNAF subdivision, 4T, shows a very definite increase in nematode infection with increase in fish size but in this area few fish were examined. In all areas where plaice were significantly infected by nematodes there is a very great decrease, with increasing fish size, in the number of nematodes per 100 lb. of fillets.

Table IX. Nematode infection rates in American plaice, 1949 to 1953, as determined by examination of the fillets. (2J-3O includes ICNAF Sub-divisions 2J, 3K, 3L, 3M, 3N, 3O.)

Length range	ICNAF Subdivision 2J-3O	3P	4R	4T	4V
cm.					
	A. Number of Fish				
6–10	2	...	...	...	...
11–20	115	34	9	21	78
21–30	463	89	169	52	136
31–40	644	42	55	34	61
41–50	651	48	13	7	31
51–60	304	43	1	2	16
61–80	45	2	...	...	2
	B. Percentage of Fish Infected				
6–10	0	...	...	...	...
11–20	0	3	22	5	3
21–30	1	1	9	19	2
31–40	0	7	9	24	3
41–50	0.2	8	15	43	3
51–60	0.3	2	0	50	0
61–80	2.2	0	...	...	0
	C. Number of Nematodes per 100 Fish				
6–10	0	...	...	...	...
11–20	0	3	22	5	3
21–30	2	1	13	21	2
31–40	0	7	9	32	7
41–50	0.2	8	31	57	3
51–60	0.3	2	0	50	0
61–80	4	0	...	...	0
	D. Number of Nematodes per 100 lb. of Fillets				
6–10	0	...	...	...	...
11–20	0	233	1,818	385	204
21–30	29	15	174	282	20
31–40	0	34	43	152	31
41–50	0.3	16	60	111	6
51–60	0.4	3	0	54	0
61–80	2	0	...	...	0
Total A	2,224	258	247	116	324
Av. of total B	0.4	4	10	20	2
Av. of total C	0.6	4	13	24	3
Av. of total D	2	12	103	166	15

Witch Flounder

Witch (Table X) are not as heavily infected as the American plaice, particularly at the smaller sizes. There may be some increase in infection with increase in fish size, but the evidence is conflicting in the case of nematodes per 100 lb. of fillets. A decrease occurs in one area and an increase in two others.

Table X. Nematode infection rates in the witch flounder, 1949 to 1953, as determined by examination of the fillets. (Areas 3K, 4R, etc., are ICNAF subdivisions.)

Length range	3K, 3L	3O, 3P	4R, 4T	4V, 4W
cm.				
	A. Number of Fish			
10–20	11	...	...	...
21–30	52	7	6	12
31–40	58	123	46	40
41–50	72	699	52	91
51–80	153	122	34	44
	B. Percentage of Fish Infected			
10–20	0	...	...	...
21–30	0	0	0	0
31–40	0	0	0	2.5
41–50	0	0.4	1.9	2.2
51–80	0	2.5	17.6	2.3
	C. Number of Nematodes per 100 Fish			
10–20	0	...	...	...
21–30	0	0	0	0
31–40	0	0	0	2.5
41–50	0	0.4	1.9	2.2
51–80	0	2.5	17.6	2.3
	D. Number of Nematodes per 100 lb. of Fillets			
10–20	0	...	...	...
21–30	0	0	0	0
31–40	0	0	0	17.5
41–50	0	1.3	5.6	6.4
51–80	0	3.2	23.2	3.0
Total A	346	951	138	187
Av. of total B	0	0.6	5.1	2.1
Av. of total C	0	0.6	5.1	2.1
Av. of total D	0	1.7	13.8	5.6

Haddock

Nematode infection of haddock fillets is so low (Table XI) that no very definite conclusions can be drawn from the material available. The infection rate apparently increases with increase in fish size but more data are needed before conclusions can be drawn regarding infection rate per 100 lb. of fillets.

Redfish

Nematode infection rates are low in redfish (Table XII), comparable with those of the haddock. As in the witch flounder, infection rates are very low in

TABLE XI. Nematode infection rates in haddock, 1949 to 1953, as determined by examination of the fillets.

Length range	St. John's	Grand Bank	St. Pierre Bank and 3P	Gulf of St. Lawrence	Nova Scotia banks: 4V, 4W
cm.					
	A. NUMBER OF FISH				
21–30	...	30	133	...	8
31–40	82	395	331	3	59
41–50	58	666	225	20	92
51–60	2	496	178	28	44
61–70	...	65	133	47	18
71–85	...	...	55	22	...
	B. PERCENTAGE OF FISH INFECTED				
21–30	...	0	0	...	0
31–40	0	0	0	0	1.7
41–50	0	0.2	0	0	2.2
51–60	0	0	0	0	0
61–70	...	0	0	2.1	5.6
71–85	...	...	0	4.5	...
	C. NUMBER OF NEMATODES PER 100 FISH				
21–30	...	0	0	...	0
31–40	0	0	0	0	1.7
41–50	0	0.2	0	0	2.2
51–60	0	0	0	0	0
61–70	...	0	0	2.1	5.6
71–85	...	...	0	9.1	...
	D. NUMBER OF NEMATODES PER 100 LB. OF FILLETS				
21–30	...	0	0	...	0
31–40	0	0	0	0	6.4
41–50	0	0.3	0	0	3.8
51–60	0	0	0	0	0
61–70	...	0	0	1.3	3.3
71–85	...	...	0	3.3	...
Total A	142	1,652	1,055	120	221
Total B	0	0.1	0	1.7	1.8
Total C	0	0.1	0	2.5	1.8
Total D	0	0.1	0	1.7	2.8

small redfish up to 25 or 30 cm. in length. There is some evidence of a small increase in infection rate of redfish with increase in fish size, but there is no good evidence of increasing infection per 100 lb. of fillets in larger fish.

SMELT

Smelt infection rates apparently increase with increase in fish size (Table XIII), but, since only one size range is well represented in the one area of high infection, no very definite statement can be made. Infection rates per 100 lb. of smelt sides (omitting from consideration the zero rates of the lowest size range examined, one sample with only 1 fish in the highest size range, and one sample with zero infection) increase with increase in fish size in two areas and decrease in two other areas.

OTHER FISHES

Modest numbers of fillets of other fishes have been examined (Table XIV). Nematodes were found in the angler, Greenland cod, pollock, yellowtail flounder,

TABLE XII. Nematode infection rates in redfish, 1949 to 1956, as determined by examination of the fillets. Labrador = ICNAF 2G, 2H, 2J; Grand Bank = ICNAF 3K, 3L, 3M, 3N; Gulf of St. Lawrence = ICNAF 4R, 4S, 4T; Nova Scotia banks = ICNAF 4V and 4W.

Length range	Labrador	Grand Bank	ICNAF 3P	N.S. banks	Gulf of St. Lawrence
cm.					
	A. NUMBER OF FISH				
9–20	5	44	198	127	8
21–25	99	122	330	170	98
26–30	215	492	321	166	32
31–35	207	762	231	192	256
36–40	131	532	175	208	404
41–65	34	266	45	25	33
	B. PERCENTAGE OF FISH INFECTED				
9–20	0	0	0	0	0
21–25	0	0	0	0	0
26–30	0	0	0.6	0	0
31–35	0.5	0	1.3	2.1	2.0
36–40	0	0	1.7	6.3	1.5
41–65	0	0	2.2	0	3.0
	C. NUMBER OF NEMATODES PER 100 FISH				
9–20	0	0	0	0	0
21–25	0	0	0	0	0
26–30	0	0	0.6	0	0
31–35	0.5	0	1.3	2.1	2.0
36–40	0	0	1.7	6.7	1.5
41–65	0	0	2.2	0	3.0
	D. NUMBER OF NEMATODES PER 100 LB. OF FILLETS				
9–20	0	0	0	0	0
21–25	0	0	0	0	0
26–30	0	0	3.1	0	0
31–35	1.5	0	3.9	6.3	5.9
36–40	0	0	3.4	13.2	2.9
41–65	0	0	2.8	0	4.0
Total A	691	2,218	1,300	888	831
Total B	0.1	0	0.7	1.9	1.4
Total C	0.1	0	0.7	2.0	1.4
Total D	0.5	0	2.9	7.3	3.6

longhorn sculpin, tomcod, and in the Greenland Halibut, *Reinhardtius hippoglossoides* (Walbaum). A total of 18 nematodes (1, 1, 4, 12) was found in the fillets of 4 of the 8 sea ravens. The infection rate of this species should be studied further.

For all these species of Table XIV there were either too few fish examined or too few nematodes found to allow definite statements to be made concerning the relation of nematode infection to the length of the fish. No nematodes were found in the fillets of 91 wolf-fish, *Anarhichas lupus* L., *Anarhichas minor* Olafsen, and *Anarchichas denticulatus* Krøyer; 38 silver hake, *Merluccius bilinearis* (Mitchill); and 16 white hake, *Urophycis tenuis* (Mitchill). All the Greenland cod, Greenland halibut, pollock and most of the wolffish were from areas of low infection of cod by nematodes. The tomcod showed a very low infection; these were adults from the estuary of the Little Codroy River, situated in the southwest corner of Newfoundland in a general area where cod are highly infected with nematodes.

TABLE XIII. *Porrocaecum* infection rate in smelt sides, 1953 to 1954. (Smelt sides, gutted, headed, skinned, vertebral column removed, estimated 63% weight of whole fish; see Fig. 17 for location of samples.)

Fish length range	Friday Bay	Valley-field	Creston Inlet	Garnish	Piccadilly Brook	Little Codroy
cm.						
	A. NUMBER OF FISH					
12–15	...	...	3	17	10	93
16–20	43	65	102	94	111	50
21–28	77	40	16	9	1	2
	B. PERCENTAGE OF FISH INFECTED					
12–15	...	...	0	0	0	0
16–20	7	5	12	2	2	0
21–28	5	3	19	11	0	0
	C. NUMBER OF NEMATODES PER 100 FISH					
12–15	...	...	0	0	0	0
16–20	9	5	18	2	2	0
21–28	7	3	31	11	0	0
	D. NUMBER OF NEMATODES PER 100 LB. OF FILLETS (SIDES)					
12–15	...	...	0	0	0	0
16–20	147	79	345	45	41	0
21–28	67	27	379	122	0	0
Total A	120	105	121	120	122	145
Total B	6	4	12	3	2	0
Total C	8	4	19	3	2	0
Total D	88	54	352	57	40	0

DISTRIBUTION OF NEMATODES IN THE FILLETS OF VARIOUS FISHES

COD

Figures 18 and 19 show the distribution of nematodes in cod fillets. The nematode distributions obtained from field and laboratory examinations were essentially similar and for presentation have been combined. Two types of fillet outline were used for record purposes, *A* during the earlier and *B* during the later part of the investigation. Type *B* represents more closely the actual fillet outline. For each type the distribution of nematodes in the fillets is essentially similar. The nematodes are embedded most frequently in the thicker portions of the fillet adjacent to the body cavity. They become scarcer further away from the body cavity, and especially posteriorly where the fillet gradually becomes thinner.

The distribution of the nematodes in the fillet agrees with the idea that they emerge through the stomach wall into the body cavity and bore into the neighbouring flesh (Scott, 1950, 1954). The apparent scarcity of nematodes at the edges of the fillet is due to the fillet, in this region, occupying only parts of the squares or as in the anterior ventral area of Figure 18A, to parts of the fillet as outlined often not being present in the actual fillet. The fillet squares corresponding to U and V of Figure 18 are usually absent, being cut off with the skin to provide a grip when the fillet is skinned.

TABLE XIV. Nematode infection rates in various fishes, as determined by examination of the fillets. Areas are ICNAF subdivisions from which the fish samples were obtained.

1. Angler
2. Greenland cod
3. Greenland halibut
4. Pollock
5. Wolf-fish
6. Yellowtail flounder
7. Sea raven
8. Longhorn sculpin
9. Silver hake
10. White hake
11. Tomcod

Fish length range	1	2	3	4	5	6	7	8	9	10	11
	Areas	Area	Areas	Areas	Areas	Areas	Areas	Area	Areas	Areas	Area
	3O, 3P	2H	3K, 3L	3L, 3N 3O, 3P	2J, 3K 3L, 3M 3N, 3O 3P, 4V	3N, 3O 3P, 4V	3O, 3P	3P	3L, 3O 3P	3L, 3P	4R
cm.	NUMBER OF FISH EXAMINED										
11–20	...	...	...	...	...	2	...	...	...	...	2
21–30	...	1	31	...	6	30	...	23	...	...	39
31–40	1	71	172	5	3	256	...	19	23	...	...
41–50	2	48	98	85	7	228	3	...	14	2	...
51–60	3	...	64	19	15	...	2	...	1	5	...
61–80	1	...	17	4	25	...	3	...	...	9	...
81–120	7	...	...	4	35	...	...	...	...	...	...
	PERCENTAGE OF FISH INFECTED										
11–20	...	...	...	...	...	0	...	...	...	...	0
21–30	...	0	0	...	0	0	...	0	...	...	2.6
31–40	0	0	0.6	0	0	0	...	10.5	0	...	...
41–50	0	2.1	.0	1.2	0	0.4	66.7	...	0	0	...
51–60	0	...	10	0	0	...	50.0	...	0	0	...
61–80	0	...	0	0	0	...	33.3	...	...	0	...
81–120	14.3	...	...	0	0	...	...	...	...	...	...

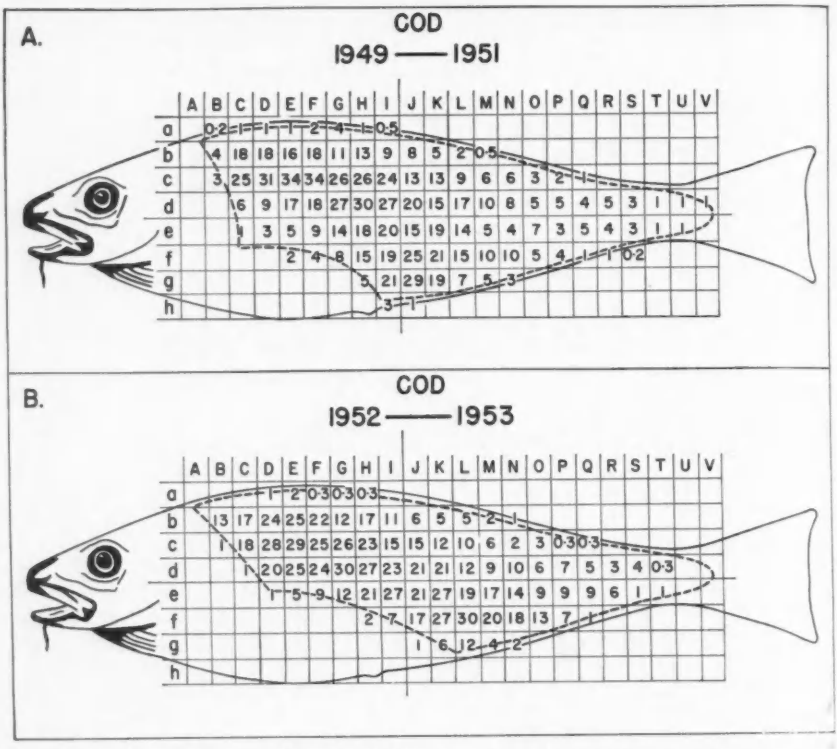

FIGURE 18. Position of nematodes in cod fillets. Number of nematodes in each square, per thousand nematodes in the cod fillet. (Actual number of nematodes observed in A, 2199 and in B, 1444. This represents the total nematodes in the fillets of over 16,000 cod.)

FISHES OTHER THAN COD

Figures 20 to 22 show the distribution of nematodes in the fillets of American plaice, witch flounder, haddock, redfish, smelt, sea raven and longhorn sculpin. There are usually more nematodes near the body cavity and certainly less toward the caudal fin, but the small numbers of nematodes do not allow such definite conclusions as are possible for the cod. In the smelt the nematodes were as large as in bigger fish and were all *Porrocaecum*; they were mainly situated in the dorsal musculature where the flesh is thickest.

SEAL DISTRIBUTION AND FOOD

Harbour seals, variously known locally as bay seals, doters or dotards, or ranger seals, are common along most of the coastline of Newfoundland and Labrador. Fisher (1950) reports them to be common also farther south, especially from Shelburne to Louisburg and Sable Island in Nova Scotia, in the Miramichi

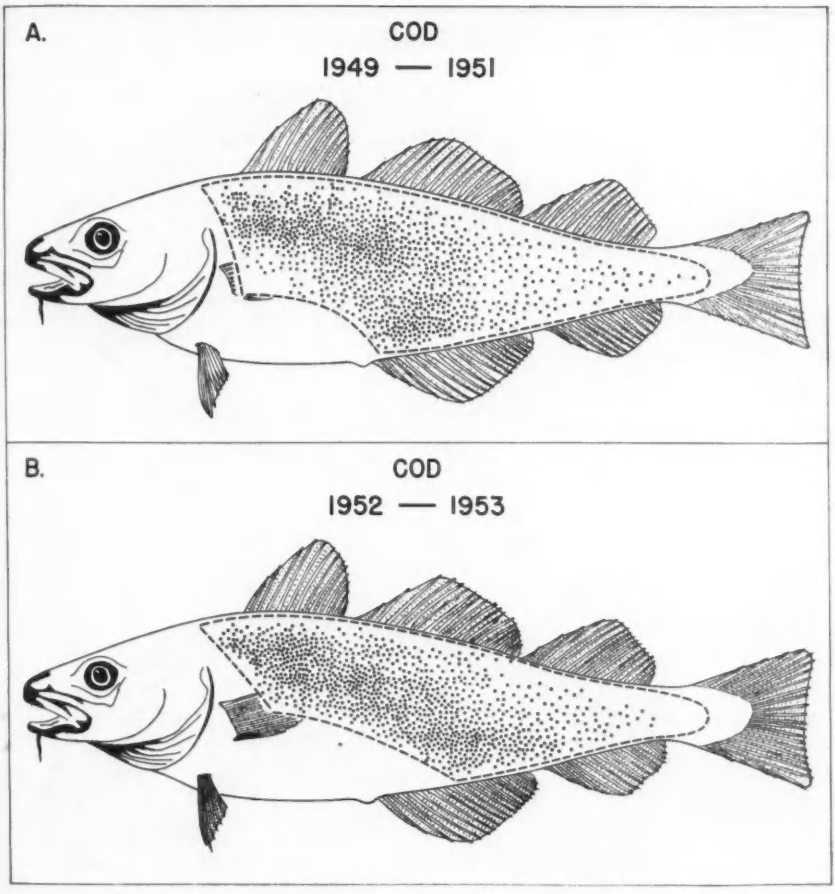

FIGURE 19. Position of nematodes, in cod fillets, per thousand nematodes in each of A and B. (Actual number of nematodes observed in A, 2199 and in B, 1444. This represents the total nematodes in the fillets of over 16,000 cod.)

estuary and on the coast below Saint John in New Brunswick, in the Pownall Bay area of Prince Edward Island, and in the Magdalen Islands.

In some parts of Newfoundland and Labrador harbour seals are hunted for their hides and meat. Recently, since October, 1952, they have also been hunted for the bounty paid by the Department of Fisheries.

The adult harbour seal is about 5 feet (1.5 m.) in length and is, therefore, recognizably smaller than the adult harp or grey seal.

Because of the harbour seal's inshore living, eating and breeding habits, and of the hunting which has gone on for centuries, some of the fishermen in an area usually have a fairly good general knowledge of the presence and location

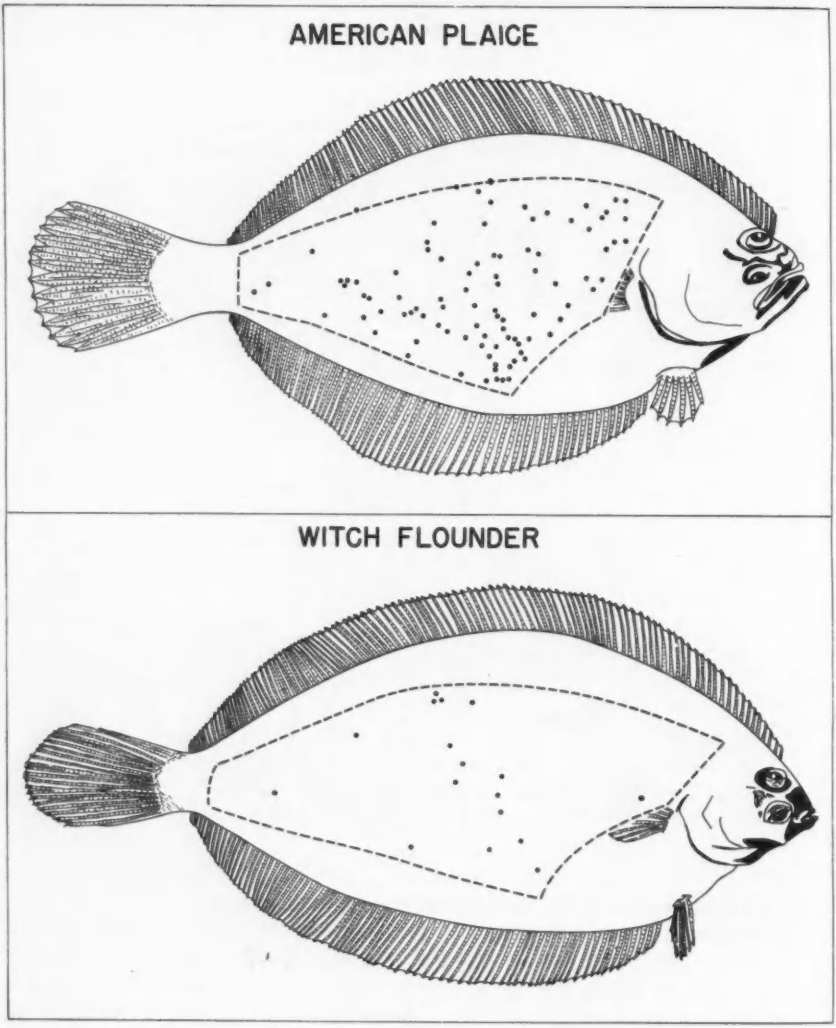

FIGURE 20. Position of nematodes in American plaice and witch flounder fillets, 1949 to 1953.

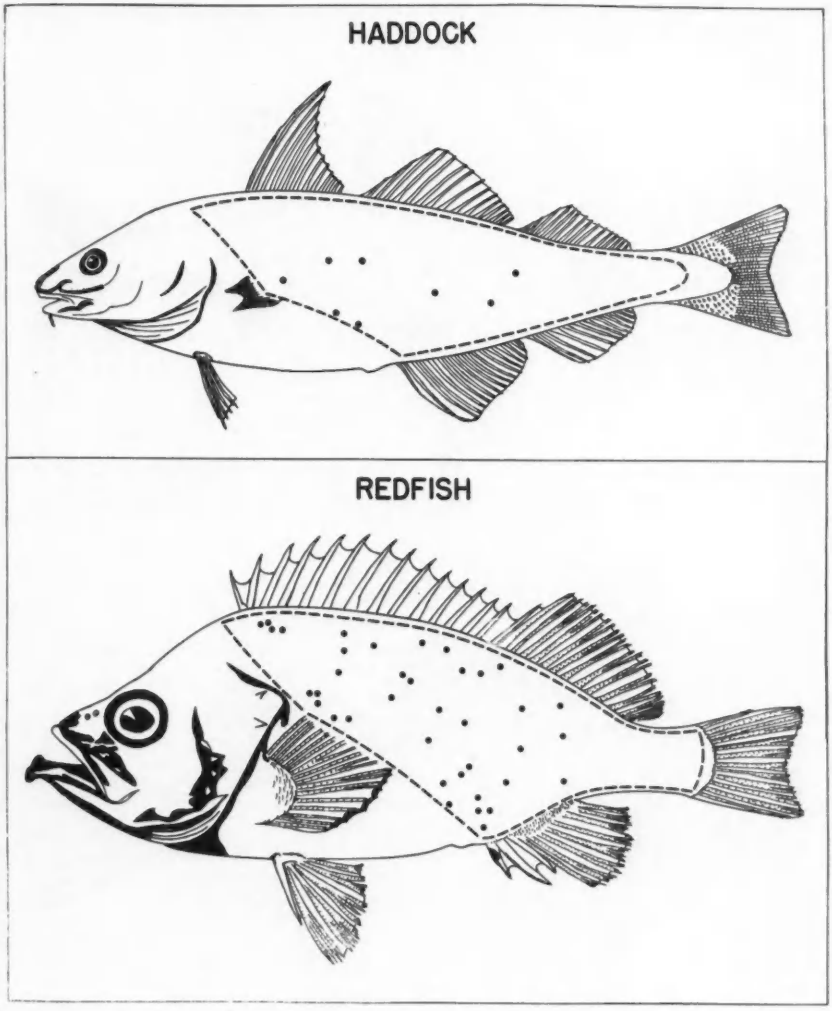

FIGURE 21. Position of nematodes in haddock fillets, 1949 to 1953 and in redfish fillets, 1949 to 1956.

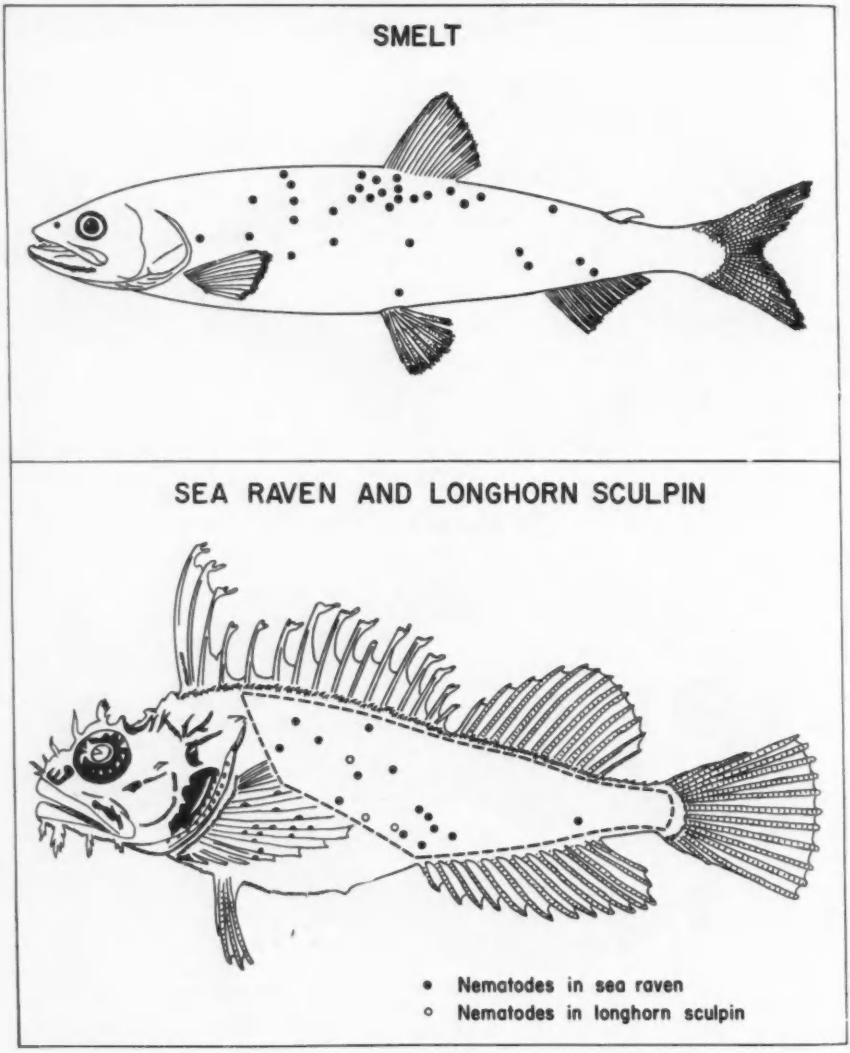

FIGURE 22. Position of nematodes in the body wall of the smelt, 1953 to 1954, and in sea raven and longhorn sculpin fillets, 1953 to 1956.

FIGURE 23. Harbour seal distribution in the Newfoundland and Labrador areas. (Includes a grey seal colony on Miquelon Island.)

of this seal. Breeding times are known approximately since the young are much more readily killed than are the older seals.

Questionnaires sent to fishermen, lighthouse-keepers, the Royal Canadian Mounted Police and others in Newfoundland and Labrador in 1950 elicited a ready response. Field parties from the Station who were doing investigations on cod in several areas, mostly during the years 1947 to 1953, were able to make observations on reported breeding places of the harbour seal and to interview fishermen regarding the occurrence of these seals. Since the bounty payments for harbour seals have begun, the jaws of seals killed for the bounty have been identified at the Station and some of this material, provided by D. E. Sergeant, has also been used in Figure 23.

NEWFOUNDLAND

The more populous areas of the east coast of Newfoundland, such as Trinity and Conception Bays and the eastern coast of the Avalon Peninsula north and south of St. John's, seem to be least frequented by the harbour seal. A fairly large breeding colony occurs in St. Mary's Bay at the Big Barachois near Little Salmonier. Breeding places are reported also at Red Head near Branch in St. Mary's Bay and at Seal Gulch in Trepassey Bay.

Occasional occurrence of the harbour seal is reported from many localities in Placentia Bay. A large colony breeding in June is reported in Creston Inlet of Mortier Bay near Marystown. A large breeding colony, estimated at about 200 seals, is reported from Cape Roger Bay and a breeding place is also reported near Nonsuch. Small numbers occur along the coast in Fortune and Hermitage Bays. Breeding places are reported at Shoal Cove Rocks in May and near Harbour Mille in June. Questionnaires from the south coast indicate the presence of occasional harbour seals as far west as La Poile Bay. At the Big Barachois near Burgeo a breeding aggregation with a fair number of harbour seals is reported to occur in June. Harbour seals ascend both White Bear River and Grey River for several miles during the summer.

Small numbers of harbour seals are said to occur along the coast in St. George's Bay, and it is possible that some breeding takes place here. Large breeding colonies occur at Shoal Point Rocks and on Long Ledges in Port au Port Bay in June. Harbour seals are reported to ascend Fox Island River. Harbour seals in fair numbers are reported from Bay of Islands with a probable colony breeding in June in North Arm. They have been seen up the Humber River as far as Deer Lake. The harbour seal is quite common along the west coast of Newfoundland from Port au Port to Flowers Cove. A large colony of about 200 inhabits St. Paul's Inlet, and these seals, breeding mainly in June, remain from May until freeze-up. They are seen in Parsons Pond and in Portland Creek Pond where a probable breeding colony occurs in late May. The Seal Rocks in St. John Bay and St. Margaret Bay, where a breeding colony of about 100 seals is reported, are possible breeding sites during the early part of June.

Breeding places are reported in Pistolet Bay about June 10, and a large colony breeds during June on the islands in the southern part of Hare Bay.

Harbour seals are common along the coast of White Bay after the northern ice floes leave the area. A possible breeding site is reported in Canada Bay, while a colony occurs in Great Cat Arm during the breeding period in June. Notre Dame Bay with all its islands and secluded coves must support a fairly large population of harbour seals. They are reported from many settlements in this bay around the rocks and islands. They are known to go into the Exploits, Gander and other rivers for some distance. Breeding colonies are reported to occur at Dildo Run, the Reach, southwest arm of Rocky Bay (Gander Bay), Edwards Reef and the Penguin Islands during late May and early June. In Bonavista Bay a large breeding colony is reported at Cat Bay, and colonies possibly breed at Shoal Arm, Seal Cove, Rocky Bay and Newman Sound from June 1 to 15. Harbour seals are reported to be rare farther south at Bonavista.

Quite a number of fishermen believe that the harbour seal may give birth to its young in many uninhabited and secluded coves around the coast where they are occasionally seen. However, considerable herds or colonies occur in the breeding season at such places as the Big Barachois near Little Salmonier in St. Mary's Bay, Creston Inlet of Mortier Bay, the Cape Roger Bay and Nonsuch area, the Big Barachois near Burgeo, Long Ledges and Shoal Point near Port au Port, St. Paul's Inlet, Hare Bay, Great Cat Arm, the Penguin Islands and Cat Bay. Other places mentioned do not seem to be as well known, or the colonies may not be as large or occur as regularly every year.

LABRADOR

Fewer reports were received from the coast of Labrador, which is sparsely inhabited, and where there is probably less knowledge of the more secluded areas, than in Newfoundland. Reports, in general, emphasized the occurrence of the harbour seal in river estuaries and often in lakes not very far from river mouths as well as along the coast and on the islands. There were reliable reports of regular and fairly large colonies at Komaktorvik (June), Double Mer (June), Rocky Bay, Hawke Bay and Alexis Bay (early June), and St. Peter Bay, in June. Most observers could not name specific places where breeding colonies occurred but were of the opinion that almost every bay or estuary, as well as some lakes near the coast, were possible breeding sites.

When a bounty for killing the harbour seal was introduced in 1952, hunting for this seal seems to have been intensified, and returns with indicated places of capture have shown substantial agreement with questionnaires concerning the location of colonies. Most returns from Newfoundland, 1952 to 1955, however, have been from the colonies at Port au Port Bay, Hare Bay and Penguin Islands. The information from the few Labrador questionnaires is greatly supplemented by returns from bounties on kills paid in 1952 to 1955. The bounty kills indicate that almost every deep fjord or bay and many smaller inlets along the coast of Labrador may have a harbour seal colony. The numbers of harbour seals taken in Hamilton Inlet were very great in 1952 to 1955. From these returns some of the largest colonies would appear to be near St. Peter Bay, Hawke Bay, Rocky Bay, Double Mer, Cape Harrison and Stag Bay. Of

course, low hunting intensity might cause low returns from large colonies, and, therefore, the number of bounty kills may not always reflect the true size of a colony.

FOOD OF THE HARBOUR SEAL

Table XV, summarizing the food of the harbour seal as indicated by the answers to our questionaires, must not be taken too literally but only as an indication of the food types. It was obvious that many of the observers had cut open harbour seal stomachs, had seen them cut open, or had obtained information from persons who had observed the contents of harbour seal stomachs. It appears from Table XV that the harbour seal is almost entirely a fish eater. In any particular region it eats the fishes which are common in the inshore area near its "hauling-out" place. These are usually the smaller fishes, although the seal will often bite a section from a salmon, at least when the salmon is in a net. In the vicinity of a seal colony many of the fishes mentioned as food could be infected by *Porrocaecum*, and a resident species, such as the smelt, is a much more likely source of infection than such a species as the

TABLE XV. Food reported consumed by the harbour seal. Figures tabulated indicate the number of times the food item in question was reported, as a percentage of the number of questionnaires mentioning food.

Food	Labrador	East Coast Nfld., C. Norman to C. Race	South Coast Nfld., C. Race to C. Ray	West Coast Nfld., C. Ray to C. Norman	Total
	%	%	%	%	%
FISH					
Herring	8	50	52	75	50
Trout	85	30	13	35	34
Capelin	39	25	13	35	26
Flounder	8	35	26	15	25
Salmon	39	28	17	20	25
Small inshore fish	15	28	22	15	22
Smelt	8	15	9	30	16
Cod	8	5	9	30	12
Greenland cod	39	13	4	...	12
Sculpin	15	8	17	5	10
Launce	15	...	4	10	5
Cunner	...	5	4	...	3
Eel	...	...	...	5	1
Eelpout	8	...	...	...	1
Pollock	...	...	4	...	1
INVERTEBRATES					
Mussel	...	10	9	...	6
Crab	...	10	...	5	5
Shellfish	...	8	4	5	5
Shrimp	...	5	...	5	3
Clam	...	3	...	...	1
Lobster	...	3	...	...	1
KELP	...	...	4	...	1
No. of questionnaires mentioning food	13	40	23	20	96
No. of questionnaires	17	96	53	31	197

capelin, which eats little other food, apart from its own eggs, during its brief spawning period inshore.

Fisher and Mackenzie (1955) describe the food habits of seals, including the harbour seal, in the Maritimes, and Fisher (1952b) gives an account of the food of the harbour seal on the coast of British Columbia. In both cases, fish made up most of the diet and the species of fish eaten depended largely on the availability of particular fish species.

General

The answers to the questionnaire indicated that, although some young harbour seals were born late in May and some after mid-June, most of the young were born during the first half of June. One Labrador observer stated that birth of the young took place in southern Labrador in June and occurred progressively later proceeding northward along the Labrador coast.

At the time of our questionnaire in 1950, two years before bounty killing began, it was the general opinion of 34% of those who answered questionnaires that the numbers of harbour seals were remaining stable around the Newfoundland coast; 48% thought that they were decreasing in numbers and 6% believed that they were on the increase; 12% expressed no opinion. In Labrador, numbers were thought to be increasing in the north but decreasing in more southerly areas.

The questionnaire reports indicated that, in the neighbourhood of the seal colonies, seals remained either all year round, or to late fall, or until the freeze-up, and in the areas where winter conditions forced them to move they appeared again in April and May.

By far the maximum concentration of harbour seals on the whole coast of Labrador and Newfoundland appears to be in the Hamilton Inlet, Double Mer, Lake Melville areas together with the neighbouring Makkovik, Cape Harrison areas to the north and the Sandwich Bay, Table Bay areas to the south.

The Federal bounty on harbour seals was first made applicable to Newfoundland and Labrador on October 16, 1952. The following information has been provided by D. E. Sergeant: In the three years October 16, 1952, to October 15, 1955, the numbers of harbour seals killed for bounty in the Newfoundland and Labrador areas were 997, 1,562 and 1,761 respectively. The kill in Labrador in these three years was 71, 65 and 67% of the total. Using jaw size as a criterion, the kill of young less than a year old was 85, 84 and 85% of the total kill in the three years respectively. Since these numbers represent the jaws presented for bounty, and since many harbour seals are killed and sink in positions or depths where they cannot be recovered, or are seriously wounded, die later and are not found, these figures are in all probability a considerable underestimate of the actual numbers killed.

Grey Seal, *Halichoerus grypus* (Fabricius)

The Biological Station at St. Andrews (FRB, 1952) reports whelping groups of grey seals:

"on Deadman Island in the Gulf of St. Lawrence, in Northumberland Strait, on Miquelon Island, along the northeast Cape Breton coast, on Sable Island, on the coast of Nova Scotia near Marie Joseph, and around Grand Manan Island. There is a seasonal movement in the spring into the Miramichi estuary, where the seals stay until early winter, and another into Bras d'Or Lakes. The grey seal on this coast pups in February".

The only certain colony at present in the Newfoundland area is on the French island of Miquelon but observations from our seal questionnaires, by D. E. Sergeant (private communication, June, 1956), and from grey seal jaws sent in for harbour seal bounty payments, indicate that, although the species is generally scarce, occasional grey seals are to be found in many parts of Newfoundland and in southern Labrador. The Miquelon colony is reported to remain there all year round.

Harp Seal, *Phoca groenlandica* Erxleben

There are two large herds of harp seals in the eastern Canadian area, one breeding in the Gulf of St. Lawrence and the other (the "Front" herd) off the northeast coast of Newfoundland and southern Labrador. These seals migrate south in late autumn and early winter and northward again to meet the floe ice and give birth to young mainly in early March. The young take to the water near the end of March and, after some further migration of the pups southwards, the main body of seals gradually works northward (being usually, according to Fisher, 1952a, north of Belle Isle by June) to spend the summer in Greenland and Canadian Arctic waters. Fisher (1952a) says that, including adults and immatures other than pups, the Gulf herd may number about a million and the larger Front herd about two million seals.

Other Seals

Smaller numbers of hooded seals, *Cystophora cristata* (Erxleben), possibly as little as 2 to 5% of the number of harps, occur off the northeast coast of Newfoundland. However, this number may be underestimated somewhat because the sealing vessels look for the large herds of harps rather than for the more scattered hoods. The hoods generally occur on heavier ice and seaward of the harps. Only small numbers of hoods whelp in the Gulf of St. Lawrence.

Occasional bearded or square-flipper seals, *Erignathus barbatus* (Erxleben), and ringed or jar seals, *Phoca hispida* Schreber, drift with the ice into the Newfoundland area. Some jar seals were reported (in answer to our seal questionnaire) to live in northern Labrador bays and to give birth to their young in April. Bounty kills of ringed seals indicate that a fair number are found in Hamilton Inlet and a few south to Notre Dame Bay. Dunbar (1949) says that, in contrast to many seal species, such as the bearded seal, the ringed seal is comparatively free of parasitic worms in the stomach and intestine. This he attributes to its habit of feeding mainly on the larger planktonic crustacea.

From the location and numbers of these three species of seals, none of them can be expected to be important in the infection of cod of the eastern Canadian area with *Porrocaecum*.

SUMMARY, DISCUSSION AND CONCLUSION

Species in the Body Musculature of Fishes

Many scientists have studied and described nematode worms found in the body musculature and elsewhere in the cod and other fishes. For the cod the literature has been well reviewed by Dollfus (1953). In the discussion following, we shall mention only the studies of most significance to the species argument, and of our own work we shall summarize mainly the parts dealing with the features of the life history of the nematodes which are or may be significant from the practical point of view of decreasing the nematode infection in fish and particularly in cod flesh.

Baylis (1916) examined the British Museum collection of a considerable number of specimens of immature ascarids from the peritoneal tissues of marine fishes. The majority of these he has referred to *Ascaris capsularia* Rud. Baylis concludes that these nematodes formerly referable to *Ascaris capsularia* are the immature larval forms of *Porrocaecum decipiens* (Krabbe). The so-called *Ascaris capsularia* larvae ranged between 9 and 38 mm. in length and possessed two divisions in the oesophagus, an anterior muscular region (pharynx) and a posterior somewhat oblong glandular region (ventriculus). In individuals below 28 mm. in length there was no indication of a caecum. In all examples from about 28 mm. upward to 38 to 40 mm. a forwardly projecting intestinal caecum was present.

Baylis (1929) describes as *Porrocaecum* or *Anisakis* sp., larval forms from fishes. These are similar to the above and have a pharynx and ventriculus like that of the adults of these two genera but without an intestinal caecum.

Dollfus (1953) records that Yamaguti (1935) found the so-called *Ascaris capsularia* in 18 species of fishes, including the Pacific cod, *Gadus macrocephalus* Tilesius. Larvae up to 34 mm. in length, without an intestinal caecum, were found. Yamaguti concludes that Baylis had included two different species in his *Ascaris capsularia*, the one without caecum being *Anisakis*, the other with a caecum *Porrocaecum*.

Again Dollfus (1953) records that Martin (1921) has made a very good study of nematode larvae found in the musculature of the cod of the North Sea. These larvae were 25 to 49 mm. long. Martin compared these, and similar nematodes obtained from the dorsal musculature of the smelt, *Osmerus eperlanus* (L.), from the North Sea, with adults of *Porrocaecum decipiens* and concluded that they were larvae of this nematode.

Kahl (1938a) also found, in cod and smelt flesh, nematode larvae 20 to 50 mm. in length with the caecum and oesophageal characteristics of *Porrocaecum*. He also found *Porrocaecum* larvae in two species of ling, *Molva molva* (L.) and *Molva byrkelange* (Walbaum); in the redfish, *Sebastes marinus* (L.); in the angler, *Lophius piscatorius* L.; and in the wolffish, *Anarhichas lupus* L. from the North Sea. These larvae were found principally in the musculature.

Wülker (1930) has found nematode larvae, 20 to 30 mm. long (in addition to *Porrocaecum* and *Contracaecum*), in a number of species of fishes from Iceland and from the North Sea. These larvae, without an intestinal caecum,

he has identified as *Anacanthocheilus* (= *Eustoma*) *rotundatus* (Rudolphi). He found this nematode in *Brosmius brosme* (Ascanius), *Gadus virens* L., *Merluccius merluccius* (L.), *Molva byrkelange* (Walbaum), *Cyclopterus lumpus* L., *Microstomus kitt* (Walbaum), *Clupea harengus* L. and *Argentina silus* Ascanius. He compared these larvae with adult specimens of *Anisakis simplex* (Rud.) but concluded that they were not *Anisakis*.

Kahl (1938b) attributes to *Anacanthocheilus* nematodes which he found in the same fish species as Wülker except that *Pleuronectes cynoglossus* L. replaces *Microstomus kitt*. In addition he has found this nematode in the cod, *Gadus callarias;* in *Scomber scombrus* L., and in *Sebastes marinus*. Many of these nematode larvae occurred in the stomach, stomach wall, mesenteries and liver. As in *Porrocaecum* some were in the body musculature. In several hundred thousand pounds of cod fillets from Iceland, Bear Island and the Barents Sea, Kahl (1939) found *Anacanthocheilus* larvae, at the rate of 2.4 larvae per 100 lb. of fillets. This compares with his finding of 2.8 *Porrocaecum* larvae per 100 lb. of fillets in a similar amount of cod fillets from the same areas. Kahl (1939) notes that in some fishes, such as mackerel and herring, the *Anacanthocheilus* larvae were usually in the body cavity and were only in the muscles when there was a high rate of infection, while in others, such as the redfish, the rate of infection by this nematode was low in the body cavity and high in the body musculature. He wonders if more than one species of *Anacanthocheilus* can be responsible for these differences, one in the body cavity and one in the muscle. Kahl (1939) also notes that, although *Porrocaecum* larvae from fishes have a maximum length of 50 mm. and are of a reddish brown colour, the larvae of *Anacanthocheilus* have a maximum length of 30 mm. and are whitish.

Baylis (1944) says that judging by Wülker's (1930) figures of the larvae from the North Sea fishes, which Wülker considers to be those of *Anacanthocheilus rotundatus*, there seems to be nothing to distinguish these larvae from those of *Anisakis* or from young larvae of *Porrocaecum*. Kahl (1938b), although believing that he can identify *Anacanthocheilus rotundatus*, does not report the morphological details on which he has relied for identification.

Punt (1941), reporting on studies of nematode parasites of many species of North Sea fishes, identifies *Contracaecum* and *Anisakis* larvae only. In measurements of 56 of these *Anisakis* larvae, Punt found a length of 13 to 26 mm., apart from one larva measuring 30 mm. which was obtained from a smelt. Punt has examined Wülker's (1930) figures and arguments and concludes that Wülker's and Kahl's so-called *Anacanthocheilus* (= *Eustoma*) larvae are in reality *Anisakis*.

Heller (1949), from nematode larvae collected from the muscles and the body cavity of the cod, *Gadus callarias*, of the Chaleur Bay region of New Brunswick, Canada, referred all the larvae with an intestinal caecum and a ventriculus to the genus *Porrocaecum*, and, although suggesting that some of the smaller larvae without caeca may also have been *Porrocaecum*, actually refers to *Anisakis* sp. all larvae possessing a ventriculus of the general *Porrocaecum* or *Anisakis* type but lacking caeca.

Scott (1953) obtained mature *Porrocaecum decipiens* by feeding living nematodes from the body musculature of each of cod, American plaice, smelt and eelpout to different young harbour seals which, from their previous feeding history and from the control animals, could be expected not to have been previously infected with *Porrocaecum*. Similarly, Scott (1956) has brought forward additional evidence that *Porrocaecum decipiens* is the only species of *Porrocaecum* in the cod.

Scott (1953), regarding nematodes examined from cod muscle, says that most of them definitely belonged to the genus *Porrocaecum* but that small specimens, presumably *Porrocaecum*, may lack the caecum and hence be indistinguishable from *Anisakis*. According to Scott (1950) the larvae of the nematode, *Porrocaecum decipiens*, in the Maritimes waters of Canada has been found to occur in cod, Greenland cod, hake, American plaice, witch, redfish, smelt, sea raven, and common eelpout, *Macrozoarces americanus* (Bloch and Schneider); but do not occur in pollock, haddock, tomcod, herring, yellowtail, nor in winter flounder, *Pseudopleuronectes americanus* (Walbaum); sand flounder, *Lophopsetta aquosa* (Mitchill); smooth flounder, *Liopsetta putnami* (Gill); and cunner, *Tautogolabrus adspersus* (Walbaum). Scott (1954) adds the following fishes to the group in which *Porrocaecum* has been discovered: the mailed sculpin, *Triglops pingeli* Reinhardt; the shorthorn sculpin, *Myoxocephalus scorpius* L.; the longhorn sculpin, the yellowtail flounder, and the winter flounder.

Scott's figure 3 (1956) indicates larval *Porrocaecum decipiens* at a total length of 8 mm. to have a caecum length of 0.2 mm. Scott found *Porrocaecum* larvae from 9 to 52 mm. in length. Dollfus (1953), regarding the related species *Contracaecum*, says that, at a length of 2 mm., *Contracaecum* larvae already possess both caeca. Lyster (1940) describes well-developed *Porrocaecum* specimens from the bearded seal in which the largest males were 9 to 11 mm. and the female 15 mm. long. In another group of more immature *Porrocaecum* from the same host the largest specimen, 1.8 mm. long, possessed a caecum. Since Lyster refers to them as *Porrocaecum*, possibly even smaller nematodes present also possessed a typical caecum.

Our studies of the length frequencies of the nematode worms from the fillets of cod, and to a lesser degree of other fishes, from the Newfoundland and neighbouring areas, indicate that two kinds of nematodes are present. The smaller nematodes have a larger percentage without a caecum while the larger nematodes are entirely of the *Porrocaecum* type. Larval nematodes without caeca from cod fillets ranged between 17–18 and 33–34 mm. and nematodes of the *Porrocaecum* type between 15–16 and 57–58 mm. in length. These lengths are slightly greater than those reported for the corresponding larval nematodes in European fish hosts, but the relative lengths of the two types in both areas are of the same order. Our *Porrocaecum* lengths also are 5 to 6 mm. beyond Scott's (1956) range. There are many factors which could produce these slight differences, for example: preservation while living or dead, various strengths of formalin, alcohol or other preserving fluids, different methods of

measuring, and actual differences between lengths of the same species of larval nematode in different areas.

It is abundantly evident that, in the body musculature of cod and many other fishes of both the Northeast and the Northwest Atlantic, there are nematodes reaching a length of 50 to 58 mm. with a forwardly projecting intestinal caecum and oesophageal characteristics of the *Porrocaecum* type and often, particularly in large specimens, possessing a reddish brown colour. It is equally evident that in the body musculature of these species of fishes there is often another nematode present, lacking a caecum, more whitish in colour and on the average smaller than *Porrocaecum*, attaining a length of 26 to 34 mm. in various areas. This type of larva possesses pharyngeal and ventricular divisions of the oesophagus similar, in the opinion of all recent workers in the Northwest Atlantic, to those of *Porrocaecum* and *Anisakis*. European workers, on the other hand, using material from the Northeast Atlantic, have variously concluded that the larval nematode without caecum was *Anisakis* (Punt), others (Wülker, Kahl) that this nematode was *Anacanthocheilus* (= *Eustoma*), and another (Baylis) was of the opinion that the larva was *Anisakis* or a young stage of *Porrocaecum* and that there was no evidence that larval *Anisakis* or *Eustoma* or young *Porrocaecum* could be distinguished.

ARE NEMATODES WITHOUT CAECA, YOUNG PORROCAECUM? Of our nematodes from cod fillets, the smaller ones, which include a high percentage without a caecum, are much more numerous, relative to the larger *Porrocaecum*, in areas such as the Grand Bank and Flemish Cap, where nematodes in fillets are scarce. In some areas there may be two modes in the general nematode frequency. Also, those without caeca have a longer pharynx than *Porrocaecum* in relation to the total length of the worm and to the ventriculus length. The caecum length in *Porrocaecum* from cod flesh is on the average greater, relative to the total length of the nematode, in the smaller than in the larger specimens. Although he does not discuss the matter, Scott's figure 3 (1956) indicates a decrease in the relative length of the caecum of the larval *Porrocaecum decipiens* with increase in relative length of the nematode from 8 to 50 mm. While, therefore, enough individual variation exists in caecum size so that an occasional individual *Porrocaecum* larva could possibly develop a caecum while in cod flesh, there is, on the whole, no support in our observations for the view of Baylis (1916, 1929, 1944) that the small nematodes without caeca in cod flesh may be young *Porrocaecum* which have not yet developed caeca.

ARE NEMATODES WITHOUT CAECA ANISAKIS OR EUSTOMA? Adult *Anisakis* of various species have been found chiefly in many cetacean species common in the Newfoundland and eastern Canadian area. All recent authors working on material in the Northwest Atlantic, whenever they have not considered the nematode larvae without caeca from cod and other fish flesh to be unidentifiable young *Porrocaecum* or *Anisakis*, have considered them to be *Anisakis*. In our larvae without caeca, from the fillets of cod and other fishes, the pharynx and ventriculus (dissected under the microscope and not sectioned) did not appear to be different from the *Anisakis* type.

Adult *Eustoma rotundata*, however, have been found in skates on both sides of the North Atlantic and in sharks of the Northeast Atlantic, and are controversially reported as larvae from the musculature of fishes from the Northeast Atlantic. *Anisakis* and *Eustoma* larvae must be present in the some host and probably in fishes from the Northwest Atlantic. Until, however, these larvae can be definitely recognized generically, or until the larvae without caeca have been fed to suitable hosts and the adults recognized, it is impossible to conclude whether some or all the larvae without caeca found in cod flesh are *Anisakis* or *Eustoma*. Since, however, the larvae without caeca, which we have examined, are similar in appearance to *Anisakis* and are not usually young *Porrocaecum*, for convenience we have referred to them as *Anisakis* sp.

Final Hosts (in the North Atlantic) of Nematodes Whose Larvae Are or May Be Present in the Body Muscles of Cod and Other Fishes

In these records of hosts of the adult parasites there is no attempt to be exhaustive but merely to provide an idea of the usual type of host of each genus.

Porrocaecum

Dollfus (1953), from various authorities, reports the following as final hosts for *Porrocaecum decipiens*: in Greenland, the harp seal, the bearded seal, the harbour seal, the ringed seal, the hooded seal, and the walrus, *Odobaenus rosmarus* (L.); on the coast of Slesvig, the harbour seal; on the Swedish coast, the grey seal. The common porpoise, *Phocoena phocoena* (L.), is also reported by several investigators as a host of *P. decipiens*.

In Canada Lyster (1940) reports *Porrocaecum* nematodes from the stomach of most bearded seals which he examined and which were obtained from localities on either side of Hudson Strait. He also reports this species of nematode from the harp seal from Stupart Bay, and from a jar seal, *Phoca vitulina*, taken at Wolstenholme. The jar seal, however, is a common name used for the ringed seal, *Phoca hispida*, so that Lyster's record is probably for this species and not for *Phoca vitulina*, the harbour seal.

Scott (1950), from a large collection of stomachs of the harbour seal and the grey seal, found that both these species were important hosts for adult *Porrocaecum decipiens*. Subsequently (FRB, 1952, 1953), the harp seal, during its winter and early spring sojourn in the Gulf of St. Lawrence, has been found to be another important host for adult *Porrocaecum*.

Scott (1953), by feeding experiments, showed that the harbour seal was a definite host of the larval worm found in the flesh of the cod, smelt, American plaice and the common eelpout. When some of these larval worms had become adult in the seals they were identified as *Porrocaecum decipiens*.

Anisakis

In the North Atlantic, *Anisakis* has been reported by various authors (Dollfus, 1953) from the common porpoise, *Phocoena phocoena*; the common

dolphin, *Delphinus delphis* L.; the white-beaked dolphin, *Lagenorhynchus albirostris* Gray; the narwhal, *Monodon monoceros* L.; the bottle-nosed whale, *Hyperoödon ampullatus* (Forster); the little piked whale, *Balaenoptera acutorostrata* Lacépède; the fin whale, *Balaenoptera physalus* (L.); the sei whale, *Balaenoptera borealis* Lesson; the false killer whale, *Pseudorca crassidens* (Owen); the blue whale, *Balaenoptera musculus* (L.); by Lyster (1940) from the white whale, *Delphinapterus leucas* (Pallas), from the St. Lawrence River and from the Canadian eastern Arctic, and by Vladykov (1944) who has noted as much as a gallon of *Anisakis* in a single stomach of a white whale from the St. Lawrence River. Baylis (1920) records the walrus, *Odobaenus rosmarus* as a host of *Anisakis rosmari* Baylis. A number of other hosts, mostly Cetacea, but one an Antarctic seal, have been recorded from the southern seas. Baylis (1932) has given a list of cetacean hosts of *Anisakis* considerably more extensive than that which we have set out above.

Eustoma rotundata (Rudolphi)

Dollfus (1953), after various authors, has reported adult *Eustoma rotundata* from the Northeast Atlantic in the alimentary canal of various species: in the skates, *Raja batis* L., *Raja fullonica* L., and *Raja radiata* Donovan; in the sharks, *Somniosus microcephalus* Bloch and Schneider, and *Carcharias glaucus* (L.). In the Northwest Atlantic Linton (1901) has reported this species of nematode in the chimaera, *Hydrolagus affinus* (Brito Capello); and in the skates, *Raja eglanteria* Bosc, *Raja erinacea* Mitchill, and *Raja ocellata* Mitchill from the Woods Hole region, Massachusetts. Heller (1949) reports this species of *Eustoma* in the little skate, *Raja erinacea*, from the Chaleur Bay region of the Gulf of St. Lawrence.

Nematodes of Importance to the Fish Trade

Two nematodes have been shown to be important parasites in cod fillets in Newfoundland and neighbouring waters. In numbers the most important of these is *Porrocaecum*, 94%. The other nematode, which we shall call *Anisakis* sp., but which may be *Anisakis* or *Eustoma* or both, has been responsible for 6% of the infection in our samples of cod fillets.

Anisakis is a small, whitish, almost flesh-coloured nematode, usually below 30 mm. in length and correspondingly thin. Apart from its small numbers and its greater abundance relative to *Porrocaecum* in offshore areas of low nematode infection, it is not believed to be a significant factor in the consumer acceptability of fillets.

Porrocaecum is, on the other hand, a large nematode, on the average almost 40 mm. in length, with very few below 30 mm. and some specimens over 50 to 55 mm. long. It is correspondingly much thicker and of much greater bulk, and with its often reddish brown colour, is much more obvious than *Anisakis*. *Porrocaecum* therefore presents the chief problem to industry in the marketing of infected cod.

Factors Affecting the Amount of *Porrocaecum* Infection in the Cod

final host distributions

References to Figures 8 to 11 and to Figure 23 shows that the high rate of infection of cod fillets with nematodes on the southern half of the west coast of Newfoundland coincides with the presence of large breeding colonies of harbour seals in Port au Port Bay and in St. Paul's Inlet. On the western half of the south coast of Newfoundland, where the nematode infection rate is comparably high, there is a breeding colony of harbour seals at the Big Barachois near Burgeo. Also, the late fall and winter outward migration of Gulf of St. Lawrence cod from the west coast of Newfoundland brings highly infected cod into this south coast area. This movement of cod has been demonstrated by tagging. The high level of nematode infection in the vicinity of the northern part of St. Pierre Bank is in the same area as the large colony of grey seals on Miquelon Island. The moderately high infection rate of cod in Placentia Bay and in the vicinity of St. Mary's Bay corresponds to the presence of colonies of breeding harbour seals in these bays.

The very great *Porrocaecum* infection in cod fillets in the southern half of the Gulf of St. Lawrence has been attributed in a general way by Scott (1950) to the presence of colonies of harbour and grey seals in that area. Great numbers of harp seals, in varying degrees infected with *Porrocaecum*, are also present here during the colder part of the year. The still greater amount of nematode infection in the Bras d'Or Lakes region of Cape Breton coincides with the presence of a wintering population of several hundred harbour and grey seals (FRB, 1952).

The high infection in the Strait of Belle Isle and its approaches can be related to the presence of colonies of breeding harbour seals in the area and probably to large herds of harp seals, somewhat infected with *Porrocaecum*, which pass northward through this area in the spring.

The low rate of nematode infection on the east coast of the Avalon Peninsula of Newfoundland and in Conception and Trinity Bays corresponds to the complete absence of breeding colonies and the usual absence of harbour seals in these areas. Northward along the east coast of Newfoundland and especially on the coast of Labrador, harbour seals appear to be as plentiful as or even more plentiful than in the coastal regions of west and south Newfoundland where high nematode infection of cod is present. However, except for the slight increase in infection in the Fogo area corresponding to a number of breeding colonies of seals in the vicinity, there is a very low nematode infection rate in this whole inshore area.

Generally, in proceeding offshore from coastal or island areas of high infection, as from the northern to the southern parts of St. Pierre Bank and from Placentia and St. Mary's Bays to the Grand Bank, the nematode infection rate rapidly decreases. The *Porrocaecum* reduction is even greater than appears in Figures 8 to 11, since a much higher proportion of the offshore nematodes is of the small *Anisakis* rather than the larger *Porrocaecum* type (Fig. 12).

Although harp seals from the Gulf herd of possibly a million seals are often infected with *Porrocaecum*, those of the larger Front herd, numbering about two million, usually have *Contracaecum* in their stomachs instead of *Porrocaecum* (FRB, 1952). *Contracaecum* sp., rather than *Porrocaecum*, is numerous in capelin (Templeman, 1948) and in many other fishes of the east coast of Newfoundland and Labrador and of the northern fringe of the Grand Bank. The large Gulf herd of harps, whose members are infected with some adult *Porrocaecum*, passes out of the Gulf on its northward migration in April and May. Presumably many of these harp seals from the Gulf herd pass northward along the Labrador coast and certainly pass through the areas of 15M, 16M, 16N and 18N, and neighbouring rectangles of Figures 8 to 10, where, however, nematode infection of cod fillets is low.

Harbour seals are moderately plentiful in northeast Newfoundland and very plentiful in Labrador, and *Porrocaecum* infection is at times high in the harp seals migrating from the Gulf of St. Lawrence northward off Labrador (southern Labrador paricularly). Thus, the very low *Porrocaecum* infection of cod fillets from northeast Newfoundland and from Labrador requires an explanation.

DISTRIBUTION OF INTERMEDIATE HOSTS IN RELATION TO TEMPERATURE

The east coast Newfoundland and Labrador areas have very much greater populations of cod than the southern Gulf of St. Lawrence and the west and south coasts of Newfoundland, and the infection from a given number of intermediate hosts may thereby be greatly diluted. The differences between areas are, however, much too extreme to be explained completely in this way. We are inclined to believe that the explanation involves the relative abundance of an intermediate host or hosts or very likely of both fish and invertebrate hosts.

The southern Gulf of St. Lawrence area, with the highest nematode infection, possesses the highest surface and inshore water temperatures of the whole eastern Canadian area inhabited by cod. The same southern Gulf of St. Lawrence, however, in the Magdalen Shallows, has very low bottom temperatures at moderate depths over most of the year. The south coast of Newfoundland, where a fairly high infection exists, also possesses, on the average, higher surface and inshore water temperatures than the east coast and still higher than those of Labrador. The Biological Station at St. Andrews (FRB, 1953) reports that experiments in 1952 suggested that long exposure to low temperature delays, and may even prevent, development of *Porrocaecum* eggs. However, from the exceedingly high *Porrocaecum* abundance in cod of the Bras d'Or Lakes of Cape Breton Island, it is difficult to believe that moderately cold water has a very unfavourable effect on the success of the early stages of the *Porrocaecum* life cycle, since the harbour and grey seals, several hundred in number, occur in these lakes only in the late autumn and winter months (FRB, 1952).

Porrocaecum is also present (Lyster, 1940) in the bearded seal in the Arctic. This is a resident seal of which only an occasional specimen drifts out of the Arctic, and, therefore, the bearded seals from Hudson Strait, which Lyster examined and of which most were infected with *Porrocaecum*, probably became

infected with *Porrocaecum* in the Arctic. A similar statement could be made regarding Lyster's report of *Porrocaecum* in the ringed seal from Wolstenholme, another resident seal, and also of the reports of *Porrocaecum* in the walrus.

Also, the infection of cod in the southern part of the Gulf of St. Lawrence is so great, in relation to the probable number of harbour and grey seals in the area, that it is easy to believe that the harp seals, which are present in the area only during the colder part of the year and have a breeding concentration usually between the Magdalen Islands and Gaspé (Fisher, 1952a), are responsible for some of the infection.

High surface temperatures and large estuaries favour the abundance of smelt which are often, especially in terms of weight, highly infected with *Porrocaecum*. The southern Gulf of St. Lawrence is by far the greatest centre of smelt abundance in the Northwest Atlantic, and the west coast of Newfoundland, from Port au Port Bay to Pistolet Bay, apparently possesses the greatest abundance of smelt in Newfoundland. While some smelt occur on parts of the east coast and in Labrador, they are apparently not generally distributed nor very numerous. Much more work, however, needs to be done on smelt infection since, as is indicated in Figure 17 and in Figures 8 to 11, areas of high nematode infection rates of cod are not always correlated with high infection rates in smelt. Smelt infection rates in terms of weight, however, are often or usually high.

The low bottom temperatures of the Magdalen Shallows in the southern part of the Gulf of St. Lawrence and on the west coast of Newfoundland favour the development of large populations of American plaice, and the small American plaice, which are often eaten by cod, are on a weight basis very highly infected (Table IX). American plaice, however, are also very common on the east coast of Newfoundland, where neither plaice nor cod are highly infected. Doubtless many other small fishes living close inshore near the seal colonies may be of importance to the *Porrocaecum* infection both in the seal and in the cod.

FISH AND INVERTEBRATES AS INTERMEDIATE HOSTS

Fish flesh has usually been subjected to gross examination on a candling table while invertebrate material is usually examined for nematodes under the microscope. Although the absence of *Porrocaecum* between the hatching length of less than 0.25 mm. (Scott, 1950) and the length of 15 to 16 mm. in Table I is not completely conclusive, it is likely that the smaller nematodes on hatching pass into an invertebrate host and grow somewhat before being passed on to a fish host.

At the Biological Station at St. Andrews, N.B., harbour seal faeces, containing eggs from adult *Porrocaecum* resulting from the feeding to the seals of larval nematodes from cod flesh, were fed to mysids, and young nematodes developed in the mysids (FRB, 1953). In a similar experiment in 1953 with a number of invertebrates, the only success was the slight growth of *Porrocaecum* larvae in the shrimp, *Crago septemspinosus* (Say) (FRB, 1954). Similar experiments in 1954 on a variety of invertebrate and vertebrate species showed positive infections for newly hatched young only in shrimp, *Pandalus* sp. (FRB, 1955).

In the feeding experiments of Scott (1953) only a very small percentage of the *Porrocaecum* fed to the harbour seals remained in the seal stomachs to become mature nematodes. Similarly there was some evidence that, even when the *Porrocaecum* nematodes became mature, within a period of several months or less the stomach of the seal could become free of nematodes. If the same results hold true in natural feeding, the harbour seal may need to be in a suitable area for good survival of the larval nematode up to the infective stage in the fish in order for the seal to become and remain heavily infected.

Scott (1950, 1954) showed experimentally that larval *Porrocaecum* from smelt, when eaten by a cod, passed through the stomach wall and into the body musculature of the cod. Thus, cod can possibly become infected by eating smaller fish containing *Porrocaecum*.

COD FOOD

We have analyzed the accumulated data at this Station on the stomach contents of about ten thousand cod from the Newfoundland, Labrador and Gulf of St. Lawrence areas. In these data we have found no clue regarding differential feeding that would explain the differences in *Porrocaecum* infection of the fillets. In any one locality, however, the cod diet varies greatly throughout the year as temperature conditions in the marine environment cause changes in the vertical distribution of the cod and as different fishes and invertebrates become available for food. Consequently, in order to compare areas properly, food studies of the cod should be made in areas of high and low nematode infection and where harbour seals are abundant. The cod apparently eats any available animal food. When schooling fish such as capelin, launce or herring are plentiful, it often feeds on them to the virtual exclusion of invertebrate food. When these are not present in numbers within its radius of daily vertical or horizontal movement, it feeds on the more solitary small bottom fishes, and on crabs, shrimp, amphipods, euphausids and other crustaceans, molluscs, echinoderms and most other available invertebrates.

Considering the relatively small infection of a large cod of 10 to 20 years of age in relation to the very great amount of food eaten during its lifetime, the practice of studying the food of the cod in order to determine the actual host which infected it may be very much like searching for a needle in a haystack. It should, however, be possible, in an area of high infection, to check for *Porrocaecum* the various species of invertebrates on which the cod is feeding. By analogy with the seal experiments it is very likely that only a few of the *Porrocaecum* larvae which enter the cod stomach find their way into the body musculature and remain there.

INFECTION OF FISHES OTHER THAN COD AND CONCLUSIONS THEREFROM ON *PORROCAECUM* LIFE HISTORY

Especially in terms of the infection per pound of fillets, the American plaice are heavily infected at the small size of 11 to 20 cm. These fish are slow-growing and this size in plaice would correspond in age to cod of a much larger size.

Witch flounders are only very lightly infected at the smaller sizes. Infection increases somewhat at the larger sizes in the areas where cod fillets are highly infected with nematodes, but the rate of infection in the witch is not high compared with that of cod. Nematode infection is at a very low rate in haddock even in areas where the cod are highly infected. Redfish, in spite of their slow growth and considerable age, similar to that of the American plaice, have low infection rates comparable with those of the haddock.

Sea ravens are highly infected; smelt are usually moderately infected individually but highly infected in terms of weight; the longhorn sculpin has a moderate rate of infection at the larger sizes; the angler, Greenland cod, Greenland halibut, pollock, yellowtail flounder, and tomcod have shown some infection, but the various species of wolffish have shown no infection. There have not been enough examinations of individuals of these species (apart from smelt) from the areas of high nematode infection in cod to make very definite comparative statements.

In addition to the fishes mentioned above, Scott (1950, 1954) has reported finding *Porrocaecum* larvae in the flesh of hake, common eelpout, mailed sculpin, shorthorn sculpin and winter flounder, but has not found them in the flesh of pollock, haddock, tomcod, brill, smooth flounder, cunner or herring. Apparently the winter flounder is usually only lightly infected.

We have found the very young witch flounder, which are much less infected than young plaice, generally in deeper water than the young plaice. The fairly heavily infected plaice population on the average is found in shallower water than the lightly infected witch and redfish. The intermediate host, if one is present between the seal and these fish is, therefore, likely to be in the shallower rather than in the deeper water. For the references to the food of various fishes in the paragraphs following, we have depended largely on Bigelow and Schroeder (1953) and on our own experience and data.

The small-mouthed flatfishes, such as the witch, yellowtail and winter flounder, which eat very little fish, show only a light nematode infection, but the large-mouthed American plaice, which eats mostly invertebrates but also at times a good deal of fish, is fairly heavily infected. This is in spite of the fact that on the average the yellowtail lives in shallower water and the winter flounder in very much shallower water than the American plaice.

The highly infected sea ravens live mostly in moderately shallow water and eat fish as well as available invertebrates, mostly bottom forms; and the Greenland halibut, living chiefly in deep water below 150 fathoms (270 m.) and with a high proportion of its diet consisting of fish, is not highly infected.

Haddock, especially when young, feed mostly on invertebrates and only occasionally on fish. Bottom invertebrates are by far the most important food of the older haddock. Immature haddock live on the offshore banks and not usually inshore, in the Newfoundland area, and they are mostly on the banks elsewhere; and haddock are very lightly infected with nematodes in the flesh. The more pelagic pollock, which feed very heavily on young fish and on pelagic crustaceans and whose young are very common near the shore, are apparently

only lightly infected. The young of these fishes, however, chiefly inhabit the areas outside the Gulf of St. Lawrence, but pollock have been common during recent years in shallow water near shore on the south coast of Newfoundland where the nematode infection of cod is moderately high.

Smelt feed considerably on Crustacea (amphipods, mysids, shrimp, etc.), to a great degree on fish fry and small fishes, and also on polychaete worms and other available invertebrates. Although *Porrocaecum* infection of individual smelt of the Newfoundland area is usually moderate, the infection in terms of weight is heavy and sometimes very heavy.

The low rate of nematode infection of individual smelt in the Piccadilly area of Port au Port Bay is rather surprising, since the very nearby Shoal Point area and the neighbouring Long Ledges area of this bay are the abodes of large colonies of breeding harbour seals. Smelt form the estuary of Little Codroy River are not infected, in spite of the presence of seal colonies 80 to 100 miles away on either side, in Port au Port Bay and the Big Barachois near Burgeo. Smelt from Fortune Bay have a low infection rate, although there are large colonies of harbour seals on the west side of Placentia Bay and grey seals on nearby Miquelon Island (40–60 miles distant). In Creston Inlet, however, where seals and smelts occupy *the same territory*, smelt are heavily infected with *Porrocaecum*. These facts indicate that the smelt, during their sea life, which is probably not wide-ranging, must be intimately associated with a primary source of infection, such as a seal colony, in order to have a high rate of individual infection with *Porrocaecum*. In 8 specimens measured, the *Porrocaecum* larvae in the smelt ranged between 33–34 and 43–44 mm., and it was obvious also from the remaining nematodes, too mutilated by the filleting operation to be measured, that *Porrocaecum* from smelt were large. There was no evidence of tiny nematodes among a total of 41 specimens, and no nematodes were found in smelt of the 12 to 15 cm. range. This argues against the direct picking up of *Porrocaecum* eggs or larvae by larval or young smelt.

The tomcod is another inshore species which, like the smelt, apparently does not disperse widely from its native estuary. Its diet is very similar to that of the smelt. The tomcod also resembles the smelt in being much more common in the Gulf of St. Lawrence than on other parts of the Canadian coast. The low rate of *Porrocaecum* infection in the tomcod sample, which was obtained from the Little Codroy Estuary in the midst of an area where the more highly migratory true cod are highly infected with *Porrocaecum*, also indicates that the site of infection of the original fish host is very close to the site of deposition of seal faeces.

The pelagically feeding herring are reported not to be infected with *Porrocaecum*, and the nematode parasites found in capelin by Templeman (1948) were mainly *Contracaecum* sp. or at least almost all possessed the *Contracaecum*-type caecum. (These nematodes were mostly found in the body cavity and below the peritoneum of the body wall and very rarely in the body musculature.) Nematodes from capelin were recently checked at this Station and most possessed the *Contracaecum*-type caecum, but a few were of the *Anisakis* type. Mr. Per

Host examined some of our nematode specimens from capelin in 1949 and identified some of them as *Contracaecum* or *Phocascaris* and others as *Anisakis* (letter, December 15, 1949). Great numbers of both capelin and herring come very close to the shore at spawning time but may not be feeding heavily at this time. Capelin stomachs during spawning season contain mostly capelin eggs (Templeman, 1948). Capelin and herring are extremely numerous which would dilute the infection. They are also pelagic feeders and bottom feeding may be necessary for the first transference of *Porrocaecum* to the fish.

CONCLUSIONS

The evidence supports the opinion that the site of infection of a fish host is localized and that heavy infections are close to a source of seal faeces. The first intermediate host, which probably exists between the seal final host and the second intermediate host, the fish, is probably somewhat sedentary and local rather than purely planktonic and widely dispersed. Apparently the larger fish may obtain much of their *Porrocaecum* infection by eating infected smaller fish. Fairly high inshore summer temperatures may be a requirement for the abundance of first intermediate hosts, and there is at present no good reason not to believe (apart from the fact that after much searching these small larvae have not been found) that the *Porrocaecum* larva would have a caecum at a small size of only a few millimetres and thus be recognized generically in its first host. If we consider the very large amount of food eaten by a large fish during its lifetime and the usually small numbers of nematodes in the fillets of an individual fish, the intermediate hosts between the seal and the larger fish would not need to be very highly infected even in the areas of high infection of fish with *Porrocaecum*.

It is possible that the low infection in such fishes as the winter flounder, the yellowtail flounder and the Greenland halibut, in the few samples examined, is due, as appears to be the case with some smelt populations, to lack of migration and absence of direct contact with the principal sites of the infection, and that with a more direct contact the level of infection would be much higher.

The above information and tentative conclusions are not entirely satisfactory, and, in order to settle many of these points, a detailed study of *Porrocaecum* infection and of the habits and food of fishes and invertebrates is required in areas of both high and low infection of cod by *Porrocaecum* and inhabited by resident harbour or grey seal populations.

Nematode Abundance in Cod Fillets in Relation to Sex and Size of the Fish

The considerable amount of data under review in this paper shows no very obvious difference between the rates of nematode occurrence in the flesh of male and female cod. Although, in the least infected areas, nematode occurrence does not become greater in cod at the larger sizes, in areas having higher numbers, the percentage of cod affected and the numbers of nematodes generally increase with size of fish. The increase in the numbers of nematodes in the flesh does not usually keep pace with the weight of the fish at the larger sizes. In almost all areas there is a decrease, at these larger fish sizes, in the number of nematodes

per pound of cod fillets. In many areas there is a continuous decrease in infection per pound of fillets from the smallest to the largest commercial sizes. In most of the remaining areas there is first of all an increase in nematode infection with size and then, at still larger sizes, either a decrease or a levelling off in infection per pound of fillets. Larger cod usually live in deeper water than the smaller cod and are thus, as a rule, farther away from the probable inshore site of much of the primary and secondary infection of fish by *Porrocaecum*.

What Steps Can be Taken to Reduce the Numbers of *PORROCAECUM* in Fish Flesh, Particularly in Cod, at the Time of Capture?

The infection of cod flesh with *Porrocaecum* is so important economically in the Gulf of St. Lawrence and its southern approaches that the scientific problem of the interrelationship of the *Porrocaecum* nematode with its fish hosts and possible invertebrate hosts should remain under study until satisfactory conclusions have been reached. There is also a real *Porrocaecum* problem with smelt and, in the Gulf area, with American plaice.

Although we cannot be certain until the complete life history of *Porrocaecum decipiens* is better understood, it is very unlikely that it will be found feasible or desirable to destroy or so seriously reduce the numbers of the small fish or invertebrate intermediate hosts as to effectively control the incidence of infection of cod flesh by this nematode.

The reduction in the size of cod which occurs when cod are intensively fished, particularly by the otter-trawl, may, at first thought, seem to offer some hope, since it is obvious that in an area of high infection both the number of cod infected and the number of nematodes in the fillets per infected cod increase considerably with increase in fish size. At the larger sizes, however, the increase in numbers of nematodes in the fillets does not usually keep pace with the increase in weight of the fish and thus, in terms of nematodes per 100 lb. of fillets, the very large fish, which are the first to be reduced in numbers by heavy fishing, usually have less nematodes than the smaller fish. It may be an illusion, therefore, except possibly in particular and limited areas, that much will be gained in terms of reducing nematode infection per pound of fillets by reduction in the size of cod. (On the other hand, unless the larger fillets are sliced, many more nematodes will remain undiscovered in the larger than in the smaller fillets after candling.) In this connection the Biological Station at St. Andrews (FRB, 1955) reports the lessening of *Porrocaecum* infection at Caraquet, N.B., since 1946, coincident with a decrease in the landed size. The cause of this reduction in nematode infection remains to be explained. There is a possibility that, with reduction of the larger sizes, cod of smaller size will become more numerous and thus dilute the amount of infection from a given number of intermediate hosts, if these are limited in their numbers available to the cod. In the Gulf, also, increases in bounty payments in recent years have probably reduced the numbers of harbour and grey seals. Additionally, during the past decade the hunting pressure on the harp seals of the Gulf has been greatly intensified.

Again, fishing in areas where the cod fillets possess less nematodes has been suggested. This practice, however, is often not posible for economic reasons, and would merely increase the pressure on the relatively nematode-free fish and allow the survival of larger numbers of highly infected fish, with the inevitable migration of many of these, under population pressure, into neighbouring relatively nematode-free areas.

There remains the possibility of a direct attack on the harbour and grey seals with the hope, faint though it may be in the Gulf, that the harp seal is not actually so important a final host as these two species. In most areas outside the Gulf of St. Lawrence the harp seal is likely to be of less importance as a host than the harbour and grey seals. It is unlikely that deliberate destruction of the great harp seal herds can be undertaken or sanctioned. There is no very good evidence yet that present harbour seal bounties are doing more than keeping the harbour seals of Newfoundland and Labrador under control. We are fairly confident, however, that in most of Newfoundland and Labrador the bounties (introduced in the Newfoundland-Labrador area in October, 1952) will in time result in a considerable reduction of the harbour seal. The grey seal of the Newfoundland area should obviously be included within the scope of this bounty.

Probably one very good area for a long-term experiment on the effect of destruction of the harbour seals would be St. Mary's Bay, Newfoundland. Here the harp seal contribution to infestation would probably not be important—because of the scarcity of this seal and because the east coast of Newfoundland harp seals have been found to carry *Contracaecum* rather than *Porrocaecum* in their stomachs. There is at least one breeding colony of harbour seals in St. Mary's Bay and these seals may very likely be responsible for the local rise in nematode infection in this area, where, in accordance with the gradual decrease in nematode infection of cod from the western and eastern parts of the south coast of Newfoundland, a further decrease would be expected. There are abundant cod and American plaice in St. Mary's Bay and many other fishes are present. There is probably a breeding colony of harbour seals in the smaller Trepassey Bay to the east, which would have to be part of the area to be treated. Some harbour seals are also killed at Chance Cove and vicinity on the southern part of the eastern coast of the Avalon Peninsula. Except for the possibility of a breeding colony at Chance Cove, the neighbouring area to the east and north (the east coast of Newfoundland from Cape Race to Cape Bonavista) is probably free of breeding colonies of seals and has a low rate of nematode infection in cod fillets. There appear to be no harbour seal colonies on the eastern side of the neighbouring Placentia Bay which lies to the west of St. Mary's Bay but there are apparently at least two breeding colonies on the western side of Placentia Bay and a colony of grey seals on Miquelon Island. The situation, therefore, is not perfect, but is probably the best in the Newfoundland area for a harbour seal-*Porrocaecum* eradication experiment. In order to show conclusive results, the experiment would need to be a very long term one with several years preliminary

study to provide a background, followed by planned eradication of harbour seals in St. Mary's Bay and in Trepassey Bay. Eradication of harbour and grey seals could then be carried out progressively from St. Mary's Bay westward, if this approach proved successful.

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The Redfish (*Sebastes marinus* L.) in the Western Gulf of St. Lawrence[1,2]

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ABSTRACT

Size at maturity and meristic characters of redfish from the Gulf of St. Lawrence are intermediate between those of the Gulf of Maine and the more northern European areas. Redfish are abundant in the Laurentian Channel in the region southeast of Seven Islands, but scarce west of this. The narrow size range (33 to 41 cm.) of the large, mature redfish taken in the Gulf of St. Lawrence is due to a southerly drift of larvae away from the spawning area, to an accumulation of old, mature fish, and to a differential distribution by sizes. The last is considered to be of primary importance. The availability of redfish on the bottom shows seasonal variations and catches were largest in the autumn. Redfish feed off the bottom and the dominant food for the sampled areas was the bathypelagic euphausiid *Meganyctiphanes norvegica*. Smaller catches of redfish at night in bottom trawls are attributed to vertical movements.

INTRODUCTION

The economic importance of the redfish in North American waters has increased greatly in recent years. It is necessary that the biology and distribution of this species be properly understood in order that the management of this fishery may be placed on a firm foundation. This paper records the results of a study undertaken by the Fisheries Research Board on some aspects of the life-history of the redfish in the western half of the Gulf of St. Lawrence.

ACKNOWLEDGMENTS

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I wish to thank the Director of the Biological Station, Grande Rivière, Quebec, for the facilities of the Station during August of 1954.

In addition, I would like to thank Captain H. H. Butler and the crew of the *J. J. Cowie*, Captain O. Lace, Jr., L. Roberts, A. C. Kohler, and all others who contributed to the collection of data in the field during the summers of 1953 and 1954.

METHODS AND MATERIALS

The fishing was carried on with the 65-foot dragger *J. J. Cowie*, belonging to the Fisheries Research Board of Canada. One sample was also obtained at sea on board a commercial trawler fishing in the Bird Rocks area in the spring of 1953.

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Field work was done in the summers of 1953 (May to October) and 1954 (May to September). Most of the field work in both years was done in the Fox River, Gaspé, Quebec, area. Samples were also obtained in the Bird Rocks area during May and September of 1953 and during May of 1954. In the upper Laurentian Channel, a series of stations was fished during July and August of 1953 (Fig. 1).

One-half hour tows were made with a 40-foot shrimp trawl or a 40-foot flounder drag to catch fish on the bottom. In 1953, the flounder drag with a shrimp net codend was used for 132 tows and the shrimp net used for 9 tows. In 1954, the flounder drag with a flounder drag codend was used for 138 tows and the shrimp net used for 50 tows.

A ½-inch (1.3-cm.) stretched mesh liner was placed in the codend of the shrimp net to catch invertebrates found near and on the bottom, for comparison with stomach contents.

Except for a few unusually large catches, all fish were examined. A random sample was taken from the large catches.

The following information was recorded for each fish:

1. Length was measured from the tip of the lower jaw with the mouth closed to the centre of the tail fork and recorded to the nearest centimetre.

2. Sex and maturity. The maturity was classed as immature, gravid or spent in the case of the females, and immature or mature for the males.

3. Parasites. The fish was examined externally for the presence of the copepod parasite *Sphyrion lumpi*.

4. Food. The stomach was opened and its contents recorded. During August–September of 1953 and May–September of 1954, representative samples of stomach contents were preserved in 5% formalin for later examinations in the laboratory.

5. Age determination. Otoliths were taken from a random sample of 101 fish and stored dry. The otoliths were broken and the readings made from the broken surface under both reflected and transmitted light.

6. Meristic characters. A small sample of fish (12) was preserved for meristic counts for comparison with other areas.

COMPARISON WITH OTHER AREAS

There is considerable confusion in the literature as to the number of valid species or forms of the genus *Sebastes* that occur in North Atlantic waters. Four species have been described, three (*Sebastes marinus* Linnaeus, *Sebastes viviparus* Kröyer and *Sebastes mentella* Travin) from European waters, and one (*Sebastes fasciatus* Storer) from American waters. *Sebastes mentella* has recently been reclassified as a subspecies of *S. marinus* (Andriiashev, 1954; Klausewitz, 1956). The *S. fasciatus* described by Storer has never been validated. Both *S. marinus* and *S. viviparus* have been reported from the northwestern Atlantic, but at the present time all redfish in this area are tentatively considered to belong to one species (*Sebastes marinus*) (Bigelow and Schroeder, 1953; Ginsberg, 1953; Goode, 1884; Jordan and Everman, 1896–1900).

The redfish (*Sebastes marinus* L.) is widely distributed in North Atlantic waters. It is found from New Jersey to Novaya Zemlya, in both coastal areas and the open sea of the North Atlantic basin. Its distribution in North American waters is imperfectly known. This is illustrated by recent records from Ungava Bay (Dunbar and Hildebrand, 1952; Tuck and Squires, 1955), and by recent discoveries of concentrations of this species in deep water off Labrador (Anonymous, 1951) and off southwestern Nova Scotia (Schroeder, 1955).

The biological and meristic characteristics of the different populations vary throughout the extensive range of the redfish in the North Atlantic. A comparison of some of these characteristics is given in Table I. The observations for the Fox River area, Gulf of St. Lawrence, are based on the results of this investigation, with the numbers of specimens examined given in italics. The observations for the other areas are derived from the literature.

The numbers of dorsal and anal rays generally are greater in the northern areas than in the southern areas. However, Ginsberg (1953) recorded counts from fish taken off Long Island, N.Y., in deep water (144–420 fathoms (263–768 m.)) which were distinctly higher than those recorded for the Gulf of Maine and the Gulf of St. Lawrence. The significance of this observation is not clear.

The early growth is similar throughout the range, except that fish in northern areas mature at a larger size than those to the south, probably because of differing ages at maturity. The fish in northern areas also grow to a larger adult size than those of southern areas.

DISTRIBUTION

Three different water layers are found in the Gulf of St. Lawrence: (1) the surface layer, with summer temperatures up to 12° C. and salinities of 29 to 32‰; (2) the cold intermediate layer with temperatures of 0 to 2° C. and salinities of 32 to 33‰; (3) bottom slope water with temperatures of 3 to 4° C. and salinities of 33 to 35‰ (Tremblay and Lauzier, 1940). The bottom slope water is found everywhere in the Gulf, at depths over 80 fathoms (150 m.). It is in this layer of water that redfish are generally found.

All commercial catches of redfish in the Gulf of St. Lawrence are made in the deep-water channels and generally at depths of over 100 fathoms (180 m.). Huntsman (1918) classified redfish as being characteristic of the warm-water layer and Jean (1955) indicated that very few fish are taken at depths of 60 fathoms (110 m.) or less in the Bay of Chaleur area. The catches of larvae as reported by Dannevig (1919), Frost (1938), and Huntsman *et al.* (1954) were confined almost exclusively to the areas over the deep-water channels. Thus it appears that redfish in the Gulf of St. Lawrence are normally found only in the deep-water channels and at depths of over 100 fathoms (180 m.).

The experimental fishing of this investigation was confined to the areas of the Laurentian Channel shown in Figure 1 and for the most part to depths greater than 100 fathoms (180 m.).

On the basis of the catches, this area can be roughly divided into two regions:

TABLE I. Comparison of the biological and meristic characters of *Sebastes marinus* from the Gulf of St. Lawrence with those of other areas. (*a*) Gill (1863); (*b*) Perlmutter and Clarke (1949); (*c*) Perlmutter (1953); (*d*) Bigelow and Schroeder (1953); (*e*) Templeman (1955); (*f*) Jensen (1939); (*g*) Williamson (1910); (*h*) Saemundsson (1952); (*i*) Kotthaus (1949); (*j*) Tåning (1949); (*k*) Lüling (1951); (*l*) Ehrenbaum (1936); (*m*) Bratberg (1955); (*n*) Andriiashev (1954); (*o*) Kotthaus (1952); (*p*) Collett (1880); (*q*) Travin (1951); (*r*) Smaragdova (1936).

AREA	Gulf of Maine	Fox River Area	Labrador (Hamilton Inlet Bank)	Iceland	Norwegian Sea	Barents Sea
MERISTICS						
DORSAL RAYS	12–15 (mean 13.5)(*a*)	13–14 (mean 13.7) *11*	...	14–17 (mean 15.3)(*g*)	13–15(1)	14–17 (mean 15.5)(*q*)
ANAL RAYS	7–8 (mean 7.1)	8–9 (mean 8.6) *11*	...	8–10 (mean 8.7)	7–9	6–10
SIZE AT 7 YEARS OF AGE	17 cm.(*b*)	...	...	...	21 cm.(*m*)	16–26 cm.(*n*, *q*, *r*)
SIZE AT MATURITY						
♂	20–26 cm.(*b*)	22–29 cm. *2,500*	...	40 cm.(*h*)	35 cm.+(*n*)	35 cm.+(*n*)
♀	23–29 cm.(*b*)	25–30 cm. *4,500*	< 37 cm. (160 fm.)(*e*) > 47 cm. (300 fm.)(*e*)			
SIZE RANGE OF COMMERCIAL CATCHES	24–34 cm.(*c*)	30–41 cm. *10,000*	...	...	30–60 cm.(*o*)	40 cm.+(*n*)
PERIOD OF RELEASING LARVAE	June–Sept.(*b*, *d*) (max. in July)	May–July (max. in early June)	June? (*f*) (in Davis Strait)	April–May(*i*)	April–May(*i*)	July–August(*i*)
SIZE OF LARVAE RELEASED	7 mm.(*b*, *d*)	7–7¾ mm.	...	7 mm.(*j*)	6 mm.(*p*)	5–8 mm.(*n*)
INCIDENCE OF *Sphryion lumpi*	1–25% (*c*)	0.09% in 1953 *3,000* 0.00% in 1954 *4,000*	8.8% at 160 fm.(*e*) 0.8% at 300 fm.(*e*)	present (*k*)	present (*k*)	...

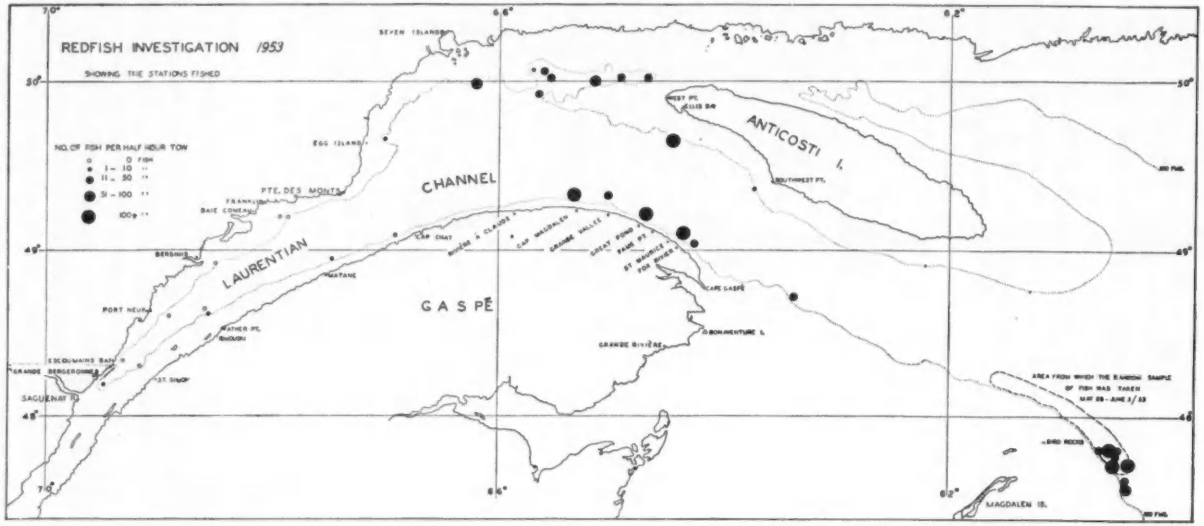

FIGURE 1. Map showing fishing stations and distribution of redfish in the upper Laurentian Channel—July and August, 1953.

(1) the region southeast of Seven Islands where redfish were abundant; (2) the region southwest of Seven Islands where redfish were scarce.

This scarcity of redfish southwest of Seven Islands agrees with the results of the experimental dragging by the Biological Station at Trois Pistoles, Quebec, as reported by Vladykov and Tremblay (1935). In their investigation, only 7 redfish were taken in this region.

The scarcity of redfish in the region southwest of Seven Islands does not appear to be related to the temperature or salinity of the water. The temperature (3° C.+) and salinity (33‰+) of the deep water of the Laurentian Channel in this region (Nadeau, 1938; Gaudry, 1938; bathythermograph records made in 1953) were similar to those of the rest of the Laurentian Channel where redfish were abundant.

LENGTH OF FISH TAKEN

The length composition of redfish taken at several stations along both sides of the Laurentian Channel is shown in Figure 2. Except for the Bird Rocks area (random sample) of 700 fish from a commercial trawler catch, May 28 to June 3, 1953), all figures are for ½-hour daylight tows made at depths between 100 and 130 fathoms (180 and 230 m.).

Except for the Seven Islands station, the fish had a very narrow size range (mostly 33 to 37 cm. for the males and 37 to 41 cm. for the females) with very few fish of less than 30 centimetres and none of less than 12 centimetres taken. In the area off the Gaspé coast (Fox River) all of the catches made throughout the summers of 1953 and 1954 had this type of size composition. Off Seven Islands, the fish were smaller but also had a narrow size range (mostly 30 to 34 cm. for the males and 35 to 41 cm. for the females).

The lack of small fish was remarkable since the gear used would have caught much smaller fish if these had been present. In addition, 60 tows were made in the Fox River area with a ½-inch (1.3-cm.) stretched mesh liner in the net, without catching any small redfish.

There are several possible explanations for this type of size composition. They are: (1) recruitment at very infrequent intervals due to a drift or high mortality of the larvae; (2) redfish are slow growing and live to an old age, with a resulting accumulation of old fish; (3) redfish of similar sizes and ages associate together and change their depth distribution with growth.

Drift of Larvae

The drift of redfish larvae in the western half of the Gulf of St. Lawrence, with special reference to the Gaspé area, was studied in the summer of 1954. Four plankton sections were located off the Gaspé coast (Fig. 3). Two types of plankton nets were used: (1) standard one-metre plankton net, mesh size #0 (15 meshes to the cm.); (2) one-metre high-speed plankton net, mesh size #xxx (9 meshes to the cm.). The standard net was towed at 2½ knots (4½ km. per hour). The high-speed net was towed at 7 knots (13 km. per hour) and later at 4½ knots (8 km. per hour) when the higher speed was found to be unsatisfactory. Oblique tows were made by fastening a 10-pound weight to the net.

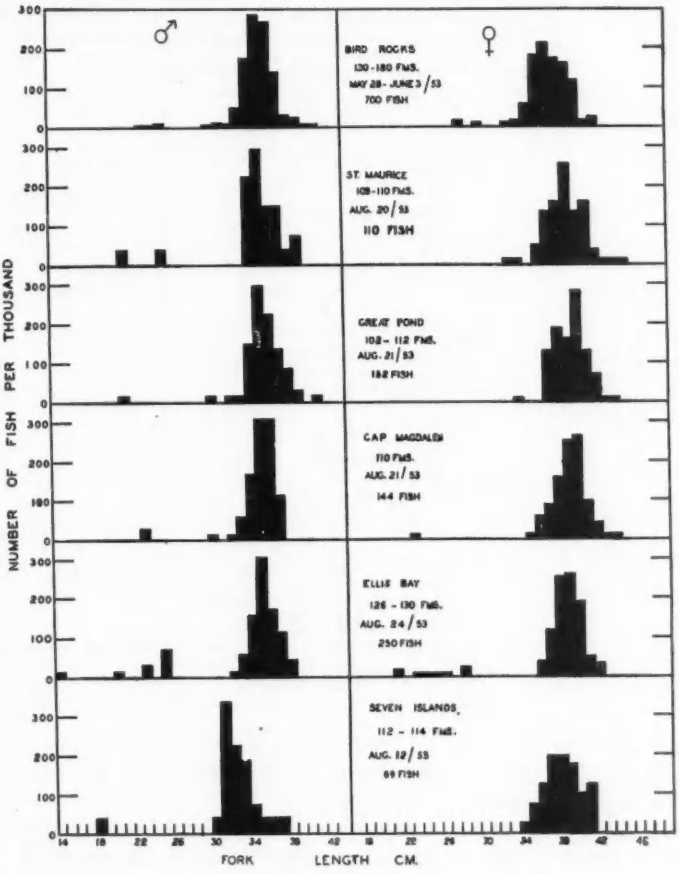

FIGURE 2. Length frequencies of redfish catches from different stations along the Laurentian Channel.

Nine plankton tows were made every other week at each section. Six surface and 3 oblique hauls were made at each section for the first 3 periods. Two consecutive surface tows were followed by an oblique haul. In the later periods, 6 oblique hauls and 3 surface tows were made. The order used for these periods was oblique, surface and oblique, etc.

Redfish larvae were preserved in 2½% formalin for later measurement. The straightened total length including the rounded tail fold was recorded to the nearest ¼ millimetre.

Examination of larvae taken from gravid females in the spring of 1954 showed that larvae of 7 to 7¾ millimetres were ready to be released or nearly so; i.e.,

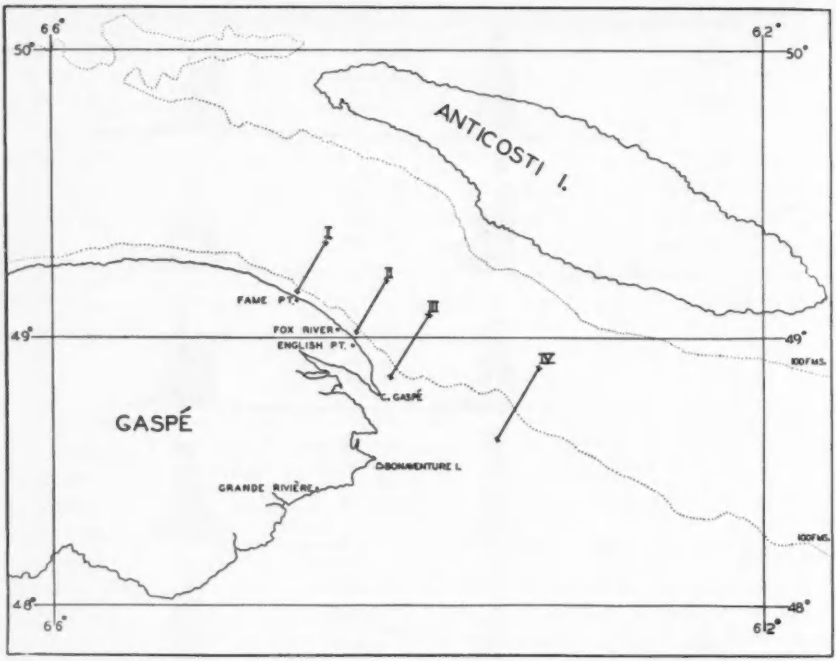

FIGURE 3. Plankton sections, 1954.

they were free in the ovary and swam when placed in sea water. Hence, all larvae larger than 7¾ millimetres taken in the plankton tows were considered as having grown after release.

Larvae were more abundant in surface than in oblique tows, indicating that the larvae live near the surface. The size compositions of the larval catches at each section for each weekly period are given in Figure 4. The catches are grouped together, irrespective of their manner of capture.

The larvae sampled increased in size from Section I to Section IV. Larvae showing growth (larger than 7¾ mm.) were taken in substantial numbers only at Sections III and IV. The presence of these older larvae at Sections III and IV is taken as evidence of southeasterly drift towards Section IV.

The catches of larvae at Grande Rivière (Jean, 1955) are further evidence of larval drift. Grande Rivière is 60 nautical miles (120 km.) from the Laurentian Channel, the nearest place where spawning redfish have been found. The implied southeasterly drift of larvae and the rapid decrease in the numbers of larvae taken in the Gaspé area, after the spawning period (Fig. 4), suggests a considerable drift of larvae away from the Gaspé area. The alternative explanation is one of a very high larval mortality in this area.

Little is known concerning the duration of the larval life of the redfish so

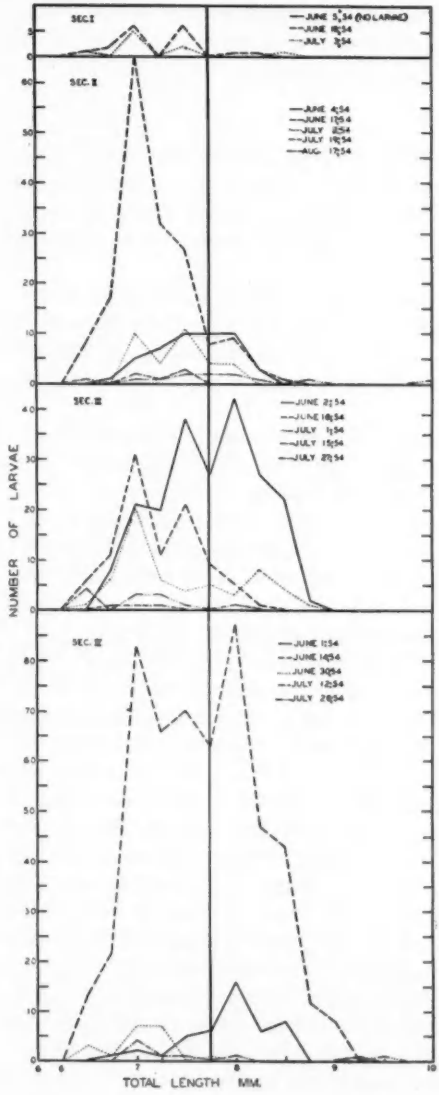

FIGURE 4. Redfish larval catches, 1954. Larvae larger than 7½ mm. are considered as having grown.

that it is impossible to determine the likelihood of all larvae being removed from the Gaspé area. However, it is possible that all larvae are killed or swept away from this area each year and that only in exceptional years is there any local recruitment to the bottom living stages.

Age and Growth

Growth of redfish has been studied by several investigators using scales, otoliths or both (Andriiashev, 1954; Bratberg, 1955; Kotthaus, 1952; Perlmutter and Clarke, 1949; Travin, 1951). Excepting Kotthaus, these authors reported that redfish grow slowly (7-year-old fish have a range of means from 16 to 26 cm.) and live to an old age.

In this investigation, age readings were made from otoliths taken from a small random sample of 101 fish. According to Bratberg (1955) one hyaline and one opaque zone of the otolith of the redfish constitute an annual ring. Age readings in this investigation were made by counting the number of hyaline zones.

The observed age-length relationship of the redfish of the Gulf of St. Lawrence is shown in Figure 5. The apparent growth is slow, with the males growing more slowly than the females at larger sizes.

The growth curve of redfish from Smaragdova (1936) and more recent data of Travin (1951) for the Barents Sea have been included in Figure 5 for comparison with that of the Gulf of St. Lawrence. The growth curve of *S. mentella* of the Barents Sea is similar to that of the redfish in the Gulf of St. Lawrence, in that they both have reduced slopes at the larger sizes. This flattening was probably due in part to a differential distribution of redfish described later and to the narrow size range of fish taken on bottom (30 to 41 cm. in the Gulf and 30 to 45 cm. in the Barents Sea). Age readings from a larger size range of fish would probably have indicated a faster growth rate. The growth curves of Smaragdova (1936) and Travin (1951) for *S. marinus* which were based on a larger size range of fish do not flatten to the same extent at the larger sizes.

Maturity studies in the Gulf (Fox River) showed that the females mature at 25 to 30 centimetres (4,500 specimens, 50% mature at 29 cm.) and the males at 22 to 29 centimetres (2,500 specimens, 50% mature at 26 cm.). Since the growth rates of the males and females are similar in the early years (Bratberg, 1955), it is believed that the females mature at an older age than the males. This is associated with the larger size of mature females.

Data obtained from growth and maturity studies show that the catches of redfish in the Gulf of St. Lawrence consist mainly of an accumulated stock of mature fish. Since the redfish fishery in the Gulf is of recent origin, this was expected. As will be outlined in the next section, however, there is still another explanation for the narrow size range available to the fishery.

Size Composition

Size compositions similar to that of the Gulf of St. Lawrence have been reported from other areas. Bigelow and Schroeder (1939) reported capturing

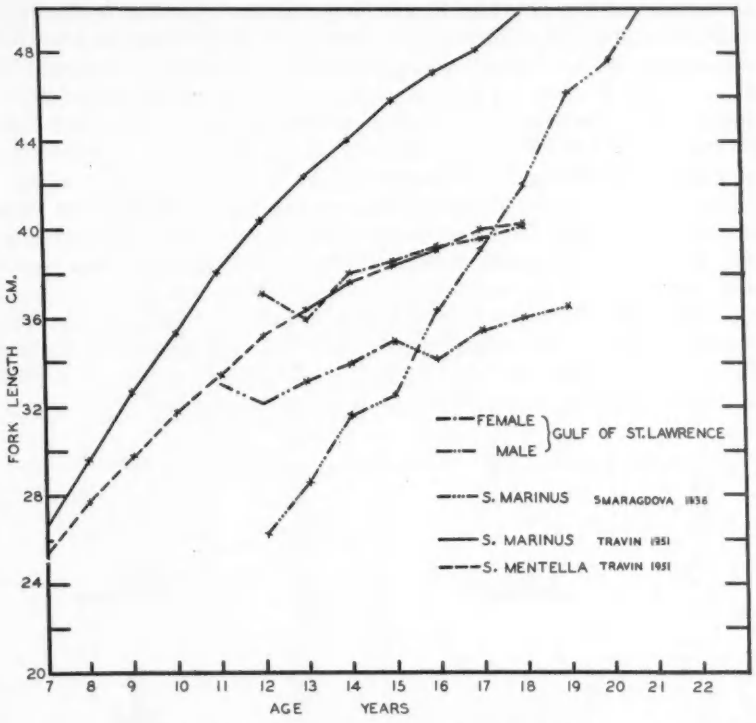

FIGURE 5. Growth of redfish (*Sebastes marinus*) of the Gulf of St. Lawrence and the Barents Sea and *Sebastes mentella* of the Barents Sea.

few redfish of less than 23 centimetres in their investigation of some of the deep areas of the Gulf of Maine. Most fish were 25 to 30 centimetres in length and the modal length was 27 centimetres. Kotthaus (1952) gave the size composition of a sample taken in the Norwegian Sea during April, 1938. Most of the fish were longer than 30 centimetres (30 to 60 cm.); few fish of 25 to 30 centimetres were taken and none were less than 12 centimetres. Schroeder (1955) reported catches from the edge of the Continental Shelf off southwestern Nova Scotia in which only a narrow size range of fish was taken (12 to 19 in. or 30 to 48 cm.). Travin (1951) noted that only a narrow size range (30 to 45 cm.) of the *mentella* form was taken in the Barents Sea. He further noted that small fish of both the *marinus* and *mentella* forms were missing in the trawl catches.

In all areas only old mature fish of a narrow size range were caught and no small fish were taken. This suggests that only portions of the populations had been captured. The size compositions of these catches can be explained if we consider the redfish as differentially distributed by size. There is considerable evidence that this occurs in the Gulf of St. Lawrence.

DEPTH DISTRIBUTION. The length frequencies of catches made at several depths on August 20, 1953, and the total catch of 6 additional tows made in June, September and October at depths between 150 and 175 fathoms (270 and 320 m.) (Fig. 6) show an increase in size of fish at depths over 130 fathoms (240 m.). Off Ellis Bay, however, this relationship was not found in the series of tows made at 110, 130 and 160 fathoms (200, 240 and 290 m.) where the size composition was similar at all depths.

Observations of larger fish in deeper water are recorded in the literature. The fish taken in deep water (Schroeder, 1955) in the area off southwestern Nova Scotia were larger than those reported from shallower water in this area (Perlmutter, 1953).

Templeman (1955) found an increase in the mean length of the fish with increasing depth in the area near the Hamilton Inlet Bank. It appeared to Templeman that redfish became adjusted, possibly at an early age, to a particular depth range and then found it difficult to move into another.

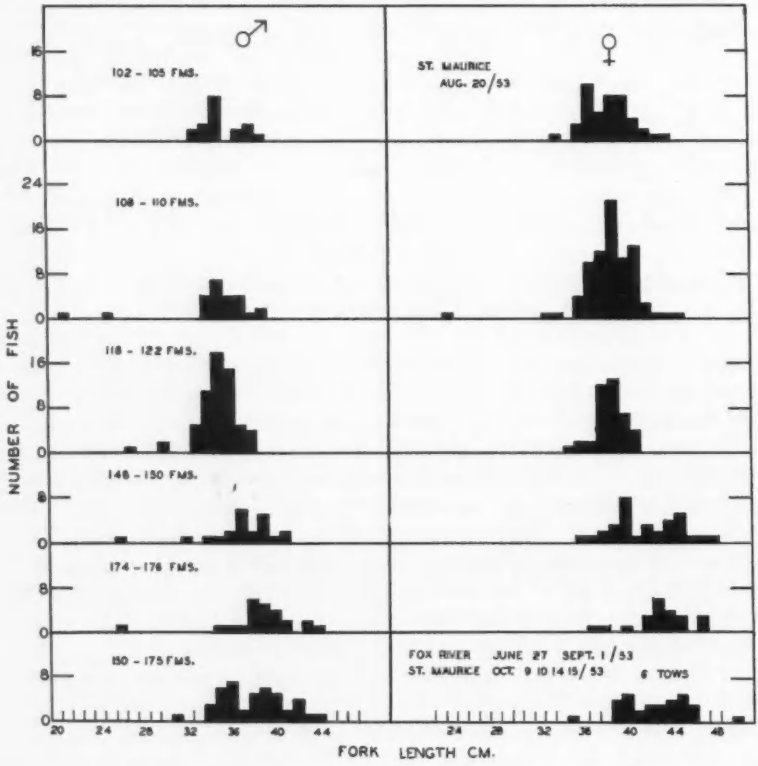

FIGURE 6. Increase in size of redfish with increasing depth in the Gaspé area, 1953.

In the Gulf of St. Lawrence (Fox River), fish from deeper water could not be distinguished from those of shallower water and hence the increase in size of fish with increasing depth in this area is interpreted as a movement of the fish to deeper water with increasing size and age.

SEASONAL CHANGES IN SIZE AT BIRD ROCKS. The size composition of redfish varied in different seasons. In spring (May 28 to June 3), a random sample of 700 fish taken on a commercial trawler was mostly large mature males (33 to 37 cm.). In September, the catches made by the *J. J. Cowie* were mainly of fish less than 30 centimetres (Fig. 7). At depths of 100 to 150 fathoms (180 to 270 m.) most of the fish taken were 23 to 33 centimetres in length. Fish of this size range were scarce in the spring sample. Two peaks are shown in the length frequency of the catches made at 150 to 180 fathoms (270 to 330 m.) and although they occur at the same sizes as the peaks of the spring catches, the

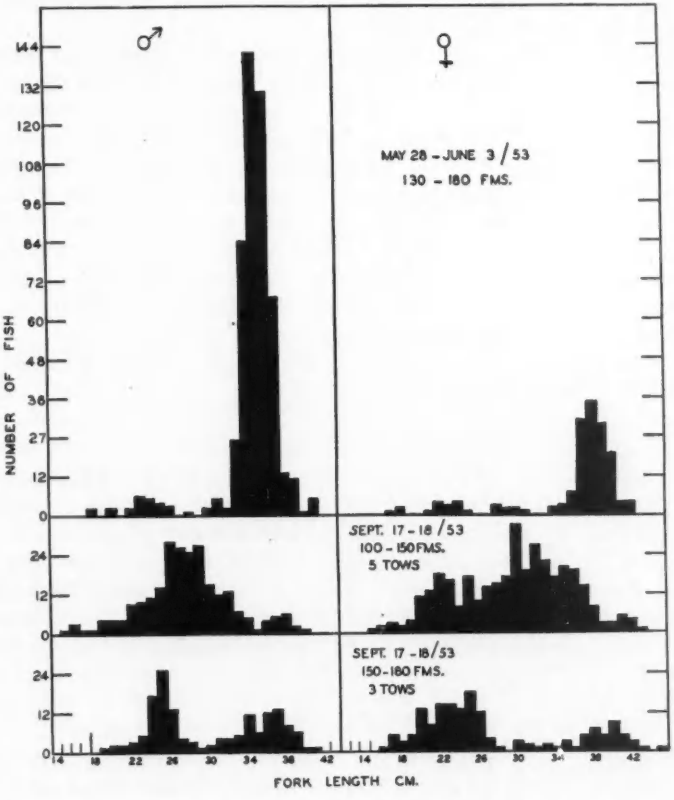

FIGURE 7. Seasonal changes in the sizes of redfish taken in the Bird Rocks area, 1953.

dominant peak shifted from large to small redfish. The 20- to 25-centimetre fish in September formed the greater proportion of the catches.

Three tows were made in the Bird Rocks area with the *J. J. Cowie* on May 12, 1954. The gear was not functioning properly and only 12 fish were taken of which 11 were mature males (34 to 39 cm.). The size composition of catches was as follows:

Length cm.	No. of males	No. of females
24		1
34	1	
35	4	
36	3	
37	2	
39	1	

Although the data are poor, it appears that the large male redfish were again present in the area in May of 1954.

The spring catches (1953 and 1954) in the Bird Rocks area were similar to the spring catches of other areas, in that mature male fish dominated the catches. The September catches, however, had an entirely different size composition from those of the spring and the autumn catches in other areas. The September catches made off the Bird Rocks are the only ones in which large numbers of fish less than 30 centimetres were taken. Off Fox River, an average catch of one small fish per tow was made during the summers of 1953 and 1954.

These observations indicate that fish of less than 30 centimetres may occur in the Gulf of St. Lawrence in significant numbers. Since their distribution is different from the large fish, it is possible that fish of the missing size ranges may be present in unsampled areas of the Gulf.

The observations of the increase in size of fish with increasing depth, and the segregation of small fish in the Bird Rocks area are evidences of a differential distribution by size. This in itself could account for the restricted size compositions which are normally characteristic of the bottom catches.

The three factors, drift of larvae, accumulation of old fish, and differential distribution by sizes, all help to explain the restricted size range of redfish taken in the Gulf of St. Lawrence catches. An accumulation of old fish is possible for all areas and has been shown to occur in the Gulf of St. Lawrence. The size range of the fish taken is, however, more narrow than would be expected if this were the only explanation. Hence, it is concluded that the differential distribution by size is the most important factor determining the narrow size range of fish taken.

SEXUAL CYCLE

The sexual cycle of redfish in European waters has recently been described by Magnússon (1955). He described the following characteristics of the reproductive cycle: (1) the testes ripen from August to January at which time they are shrunken and yellowish in colour; (2) copulation takes place between October

and January; (3) the bladder secretes a fluid which apparently functions in sperm transfer; (4) the size of the bladder shows seasonal variations according to the amount of fluid present and is largest from October to January; (5) the eggs are small and unripe when copulation occurs. The sperm is retained in the ovary until February when the eggs reach their maximum size and are fertilized; (6) the larvae are released in May; (7) the testes are largest and whitest in May–July at which time they are unripe.

Field observations of the relative size of the male bladder, and of the gross appearance of the testes and ovaries at different seasons fit the pattern described by Magnússon. Thus, it is assumed that the sexual cycle of the redfish in the Gulf of St. Lawrence is similar to that of European waters, although the timing of the various stages may differ. The period of releasing larvae in the Fox River area as determined by an examination of mature females (Table II) and from catches of larval redfish (Fig. 4) was found to occur from May to July with the peak period in early June.

TABLE II. Percentage of mature females which were gravid in the bottom catches made off Fox River, 1953 and 1954.

1953	No. of mature females	Percentage gravid	1954	No. of mature females	Percentage gravid
June 18–19	26	50	May 27–28	39	82
June 25–30	136	12	June 8–11	37	41
July 4–9	124	1	June 21–26	98	6
Aug. 18–20	263	0	July 8–9	71	1
			July 22	20	5
			Aug. 19–20	31	0

SEASONAL VARIATIONS IN AVAILABILITY IN THE FOX RIVER AREA

The average catch per ½-hour tow in 1953 increased progressively from a low level in June to a high in October (Fig. 8). Catches were small again when fishing was resumed in May, 1954, and the numbers increased slowly to a high in September. The increase which occurred in 1954 was much less than that of 1953. The reason for this is not clear. Males outnumbered females in the catches of May, June and July and females outnumbered males in the catches of August, September and October. Mature females had the greatest relative increase, both in 1953 and 1954.

The increase in availability from spring to fall in bottom trawling was probably general over the whole area from Seven Islands to the Bird Rocks. In May, June and July, mature males outnumbered the mature females in the catches made off Fox River, Cape Gaspé and the Bird Rocks. In August and September, mature females outnumbered the mature males in the catches made off Fox River, Seven Islands, Ellis Bay and Cape Gaspé. Thus, it appears that the changes in the sex ratio, such as were found off Fox River, were general over the whole area. If such is the case, it would appear that the changes in availability are due to vertical rather than to horizontal movements of the fish.

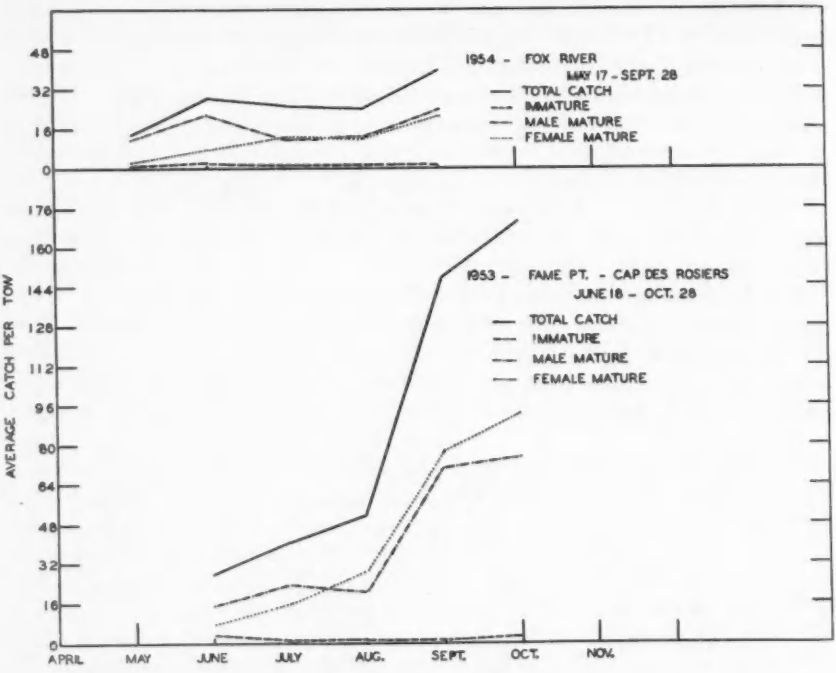

FIGURE 8. Seasonal variations in the size of the bottom catches of redfish in the Fox River area, 1953 and 1954.

These vertical movements can be related to the sexual cycle. As the period of copulation approached (October to January) and the gonads ripened, the availability of fish on the bottom increased. At this time, females slightly outnumbered males in the catches. In the spring (May and June), females were scarce on the bottom and the catches consisted almost entirely of mature males. Thus, at the time when the larvae were released, most of the females were probably pelagic.

Catches with an uneven sex ratio have been noted in European waters by Kotthaus (1949), Magnússon (1955) and Williamson (1910). This may indicate similar seasonal vertical movements in European waters.

FEEDING HABITS

Mature male redfish ceased feeding from late July until observations were terminated in October, 1953, and September, 1954. The cessation of feeding was related to the ripening of the gonads of the mature male fish. The immature males and the mature females during the same period (July to October) were feeding actively (Table III).

TABLE III. Seasonal changes in the feeding habits of redfish, 1954.

Period	Mature males		Immature males		Mature females	
	No. examined	Percentage with food	No. examined	Percentage with food	No. examined	Percentage with food
May 17–July 22	1,171	64	28	47	364	53
Aug. 19–Sept. 17	419	2	17	47	648	75

FEEDING HABITS AND THEIR RELATIONSHIP TO REDFISH DISTRIBUTION

The results of the analysis of species and volume of food in 211 stomachs are given in Table IV and Figure 9. Euphausiids, and especially *Meganyctiphanes norvegica*, were the dominant food items in redfish stomachs, with amphipods, shrimp, fish and copepods of lesser importance. Pelagic forms (21 of the 32 species of food organisms) were most commonly found in stomachs and made up most (over 90%) of the volume of the contents. The occurrence of deep-water copepods and fish in stomachs shows that even though redfish feed off the bottom, they tend to remain below the intermediate cold-water layer.

Pelagic animals have also been found to form most of the food of redfish in the Barents Sea (Andriiashev, 1954) and in Newfoundland waters (FRB, 1954).

DIURNAL VARIATIONS IN THE SIZE AND COMPOSITION OF THE CATCHES

Commercial fishermen report that redfish are not as abundant on the bottom at night as they are in the daytime. To investigate this phenomenon, comparable day and night tows were made in the Fox River area from June to September of 1954.

TABLE IV. Analysis of redfish stomachs from Saguenay River to Cape Gaspé in 1953 and from Fox River in 1954. Numbers and percentages of feeding fish containing each type of food are recorded by species groups in field examinations and by species in laboratory examinations.

	1953 Saguenay River–Cape Gaspé				1954 Fox River			
	Field		Laboratory		Field		Laboratory	
	No.	%	No.	%	No.	%	No.	%
Total no. stomachs	2,645	...	...	...	4,096	...	...	...
No. everted	61	2.4	...	...	334	8.1	...	...
Net no. stomachs	2,584	...	...	...	3,762	...	...	...
No. empty	1,151	44.5	...	...	1,133	30.1	...	...
No. feeding	1,433	55.5	80	...	2,629	69.9	131	...
EUPHAUSIACEA	1,304	90.9	69	87	2,571	97.8	125	95
Meganyctiphanes norvegica[c]	...	...	66	84	...	...	124	95
Thysanoessa inermis[c]	...	...	35	44	...	...	21	16
Thysanoessa raschii[c]	...	...	27	34	...	...	5	4
Thysanoessa longicaudata[a,c]	...	...	1	1	...	...	0	0
COPEPODA[e]	127	8.8	57	72	263	10.0	84	64
Calanus finmarchius[c]	...	...	8	14	...	...	4	3
Calanus hyperboreus[c]	...	...	32	41	...	...	19	15
Euchaeta norvegica[c]	...	...	56	71	...	...	82	63
Metridia longa[c]	...	...	5	6	...	...	3	2
Gaidius tenuispinus[c]	...	...	1	1	...	...	0	0
Halithalestris cronii[c]	...	...	0	0	...	...	1	0.7

TABLE IV. (*Continued*)

	1953 Saguenay River-Cape Gaspé				1954 Fox River			
	Field		Laboratory		Field		Laboratory	
	No.	%	No.	%	No.	%	No.	%
AMPHIPODA[e]	179	12.5	53	67	377	14.3	91	69
GAMMARIDEA	1	0.07	1	1	2	0.08	1	0.7
Anonyx nugax	...	...	...	...	...	...	1	0.7
CALLIOPIIDAE[a]	...	...	1	1	...	...	0	0
HYPERIIDEA[e]	179	12.5	53	67	377	14.3	90	69
Themisto gaudichaudi[c]	...	...	32	41	...	...	33	25
Themisto abyssorum[c]	...	...	49	62	...	...	78	60
Hyperia galba[c]	...	...	1	1	...	...	0	0
DECAPODA	37	2.6	7	9	117	4.5	36	27
Pasiphaea multidentata[c]	...	...	4	5	...	...	35	27
Pandalus borealis	...	...	2	3	...	...	3	2
Pandalus montagui	...	...	0	0	...	...	3	2
Pontophilus norvegicus[d]	...	...	1	1	...	...	0	0
MYSIDACEA	1	0.07	1	1	3	0.1	3	2
Boreomysis tridens[d]	...	...	1	1	...	...	3	2
Amblyops abbreviata[d]	...	...	0	0	...	...	1	0.7
ISOPODA[e]	0	0	1	1	0	0	3	2
Munnopsis typicus	...	...	1	1	...	...	3	2
ANNELIDA (POLYCHAETA)	2	0.1	1	1	0	0	0	0
Leanira tetragona[d]	...	...	1	1	...	...	0	0
CHAETOGNATHA[e]	23	1.6	13	16	1	0.04	1	1
Sagitta elegans[a,c]	...	...	2	3	...	...	...	...
Unidentifiable	...	...	13	16	...	...	1	1
COELENTERATA (MEDUSAE) (*Aglantha digitale*)[a,c]	...	...	6	8	...	...	15	11
CTENOPHORA (*Pleurobrachia* sp.)[a,c]	...	...	4	5	...	...	1	0.7
COELENTERATA AND CTENOPHORA[e]	75	5.2	...	...	53	2.0	...	...
MOLLUSCA	1	0.07	1	1	3	0.1	3	2
Pteropoda	0	0	0	0	3	0.1	3	2
Clione limacina[c,d]	0	0	0	0	3	0.1	3	2
Cephalopoda	1	0.07	1	1	0	0	0	0
Ilex illecebrosa[a,c,d]	1	0.07	1	1	0	0	0	0
PISCES	58	4.0	6	8	15	0.6	3	2
Paralepis rissoi kroyeri[c]	11	0.8	2	3	5	0.2	2	1
Clupea harengus[c]	1	0.07	0	0	0	0	0	0
Melanostigma gelatinosum[b,d]	2	0.07	0	0	0	0	0	0
Euchelyopus cimbrius[a]	0	0	0	0	1	0.04	1	0.7
Unidentified and unidentifiable	44	2.1	3	4	9	0.3	2	1
INSECTA	...	...	...	...	1	0.04	...	...

[a]identification doubtful
[b]tentatively identified as this species
[c]pelagic species
[d]of unusual occurrence and selected for that reason so that the frequency of occurrence in the table is unrepresentatively high
[e]small and fragile specimens which may have been missed in the field notes with the result that the indicated frequency of occurrence is probably lower than the actual

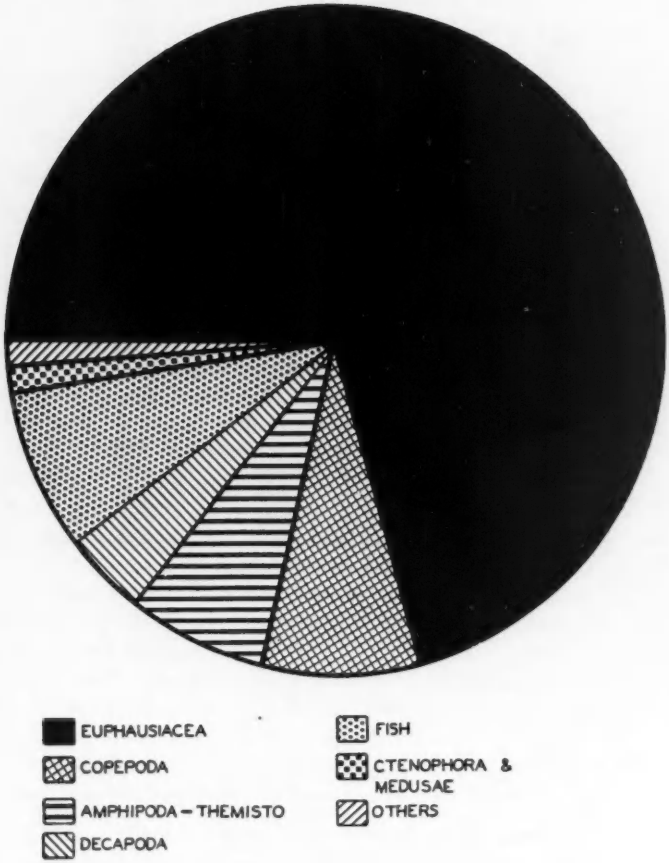

FIGURE 9. Proportions, by volume, of different species groups in 80 large redfish taken from the Saguenay River-Cape Gaspé area during 1953.

The day was divided into four periods as follows: (1A) noon to sunset; (1B) sunset to midnight; (2A) midnight to sunrise; (2B) sunrise to noon. The procedure used was to make tows in the 1A (afternoon) and 1B (after sunset) periods during one week and tows in the 2A (before sunrise) and 2B (morning) periods during the following week. The tows were all made at approximately 110 fathoms (200 m.) and as far as possible, all were made in the same area. The grouped results for the whole period from June to September are given in Figure 10.

Catches of redfish were less in the night periods (1B, 2A) than the catches made in the day periods (1A, 2B). The sexes behave somewhat differently.

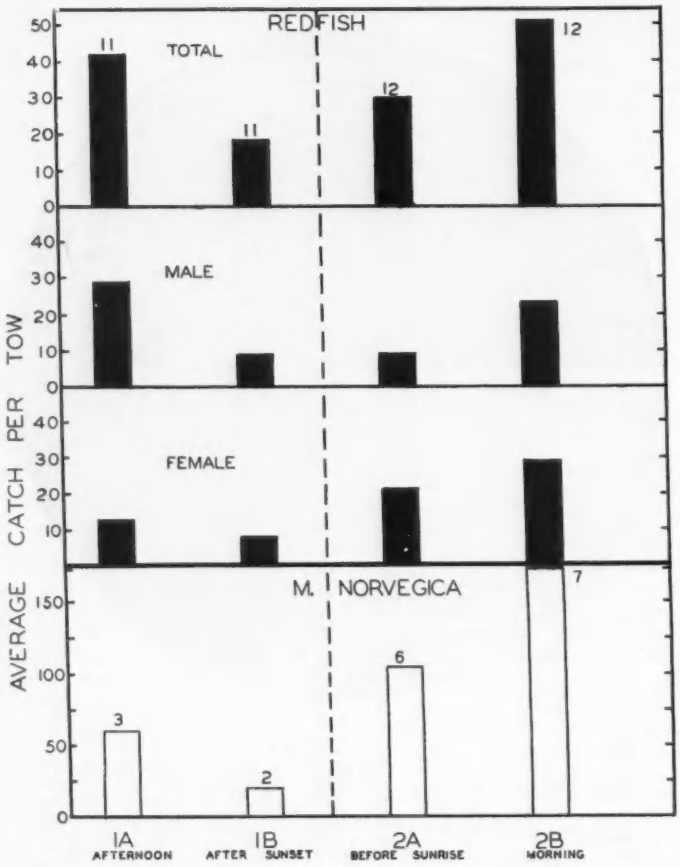

FIGURE 10. Diurnal variations in the average catch per ½-hour tow of redfish and *M. norvegica* in the Fox River area, 1954. The number of tows is shown.

An attempt was made to correlate the availability of redfish with that of *M. norvegica* because of its importance in the diet of redfish in the Fox River area. Catches of *M. norvegica* were likewise smaller in the night catches (Fig. 10). This observation is in general agreement with the observations of Fowler (1905) and Macdonald (1927) who demonstrated vertical movements of *M. norvegica*.

Changes in availability of redfish on the bottom might be due to them following *M. norvegica*. When the mature males were not feeding (late July to October) however, they still underwent diurnal changes in availability. Thus it appears that the vertical movement may be influenced in part by changes in light intensity.

It is concluded that the changes in availability on the bottom were due to vertical movements of the fish. Male redfish evidently leave the bottom after sunset and return about sunrise. The behaviour of the males when they are not feeding suggests that the vertical movements are a response by the fish to changes in light. This may be modified when the fish are feeding by a search for food. Female redfish leave in the afternoon and return following sunrise, following closely the pattern of *M. norvegica.*

Depth Distribution

In the Fox River area, a correlation between increasing depth and decreasing numbers of redfish was observed for the immature and mature males, and for the mature females in 1954 at depths between 100 and 175 fathoms (180 and 320 m.) (Table V). This depth distribution of redfish is correlated with that of the dominant food, *Meganyctiphanes norvegica.* This euphausiid decreased in number with increasing depth (Table VI). The other common invertebrates in bottom tows were unimportant as redfish food, and their depth distribution differed from that of *Meganyctiphanes.* The two shrimps (*Pasiphaea multidentata* and *Pandalus borealis*) were apparently distributed independently of depth. The mysid *Boreomysis tridens* increased in number with increasing depth.

The importance of food in the depth distribution of refish was further examined by a study of changes in redfish food at different depths (Fig. 11). Euphausiids were almost the only food at depths where redfish were caught in greatest numbers. *Meganyctiphanes* was ot negligible importance in the diet of scarce, deep-water redfish.

In other areas, the decrease in numbers of redfish with increasing depth between 100 and 175 fathoms (180 and 320 m.) was not found to the same

Table V. Distribution of redfish with depth in the Fox River area, June–September, 1954. Average catch per tow and the range of catches (in brackets) are shown for the depth intervals indicated.

Depth range (*fathoms*)	105–115	115–125	125–135	135–175
No. of tows	43	38	27	11
Total	38 (7–128)	28 (2–64)	14 (1–47)	11 (0–14)
Immature	1 (0–4)	1 (0–3)	0 (0–4)	0 (0–2)
♂ Mature	20 (3–70)	15 (1–36)	10 (1–25)	6 (0–2)
♀ Mature	17 (1–58)	12 (0–28)	4 (0–22)	5 (0–1)

Table VI. Distribution of some common invertebrates with depth in the Fox River area, July–September, 1954. Average catch per tow and the range of catches (in brackets) are shown for the depth intervals indicated.

Depth range (*fathoms*)	105–115	115–125	125–150
No. of tows	11	6	3
Pasiphaea multidentata	8 (0–22)	14 (1–37)	12 (4–23)
Pandalus borealis	9 (0–22)	11 (1–32)	11 (4–22)
Meganyctiphanes norvegica	141 (7–485)	77 (20–229)	27 (9–51)
Boreomysis tridens	40 (0–167)	87 (4–246)	289 (3–716)

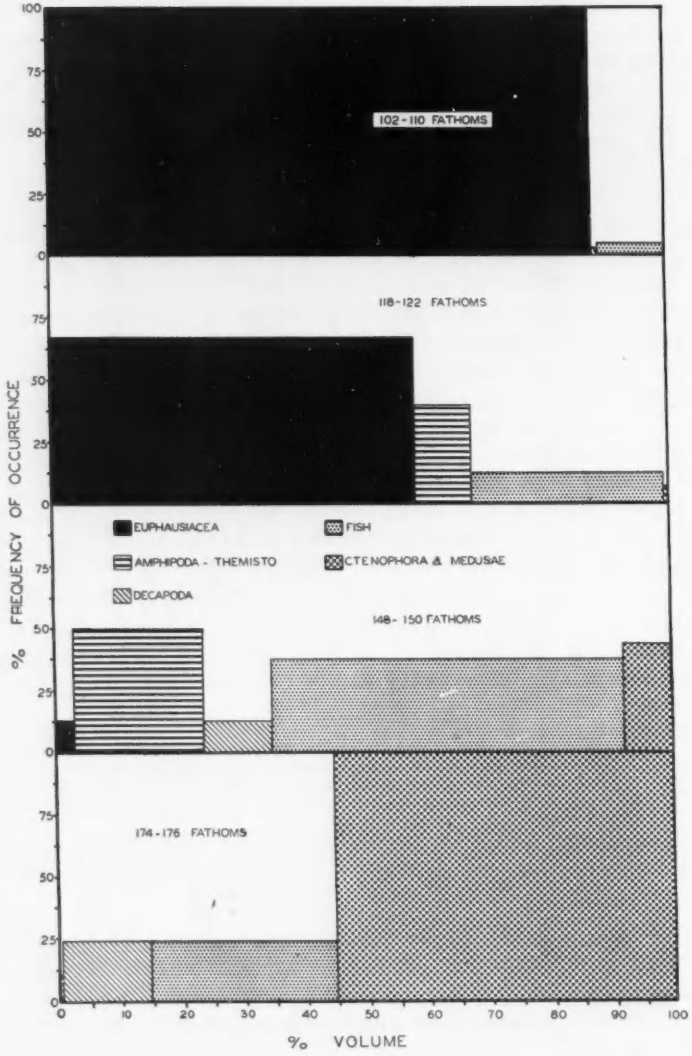

FIGURE 11. Changes in redfish stomach contents with increasing depth, August 20, 1953.

extent. Off Ellis Bay, Anticosti Island, the best catch was made at 130 fathoms (240 m.) and fewer fish were taken at both 110 and 160 fathoms (200 and 290 m.).

Templeman (1955) reported making the best catches off Hamilton Inlet Bank at 200 fathoms (400 m.). The catches decreased with both increasing and decreasing depth. Schroeder (1955) reported catching redfish down to 425 fathoms (777 m.) off southwestern Nova Scotia with the best catches at 200 and 300 fathoms (400 to 500 m.).

Redfish have a wide depth range (10 to 400+ fathoms or 20 to 730 m., Bigelow and Schroeder, 1953), but in any particular area they have their greatest concentration at a particular depth. In the Gaspé area of the Gulf of St. Lawrence, this depth distribution appears to be correlated with the abundance of the food organism *M. norvegica.*

SUMMARY AND CONCLUSIONS

All redfish of the Gulf of St. Lawrence are tentatively included in the species *S. marinus.* This species is found from Novaya Zemlya to New Jersey. The meristic characters, size at maturity and adult size of the redfish in the Gulf of St. Lawrence are intermediate between those of the small redfish of the Gulf of Maine and the large redfish of northern European waters. The growth rate before maturity is similar throughout the range of the redfish but there are large differences in growth among different populations of mature fish. In northern areas the larger adult size may be related to the larger size at maturity.

In the Gulf of St. Lawrence, redfish are normally found only in the Laurentian Channel. They are abundant in the region to the southeast of Seven Islands but are scarce west of this. This restricted distribution is not due to the temperature and salinity of the water since these conditions are similar in both areas. The possible effect of the availability of food may be inferred from its demonstrated effect on the vertical distribution of redfish.

A narrow size range of old mature fish (males 33 to 37 cm. and females 37 to 41 cm.) was taken in the catches. Three factors are offered to explain this size composition: (1) recruitment at infrequent intervals due to a drift or high mortality of larvae; (2) accumulation of old fish; (3) differential distribution of redfish by sizes. A southerly drift of larvae was shown to occur in the Gaspé area, but it is doubtful if this factor could account for the narrow size range of redfish found in the bottom catches of other areas. Growth and maturity studies show that the catches are composed of a stock of old mature fish. However, this factor does not explain the complete lack of small fish or the extreme narrowness of the size composition. The presence of larger fish in deeper water off Fox River and the presence of smaller fish in the Bird Rocks area in September show that differences in distribution of redfish by sizes occur in the Gulf. This factor could in itself explain the narrowness of the size range of the fish taken. It is concluded that the three factors, drift of larvae, accumulation of old fish, and differential distribution, all affect the size composition and that the latter factor is of primary importance.

The sexual cycle has important effects on the distribution and feeding of redfish. Larvae are released during May, June and July with the peak period in early June in the Fox River area. At this time, mature redfish, especially the females, are scarce on bottom throughout the Gulf of St. Lawrence and it is probable that the females normally release their larvae in mid-water. As the gonads ripen, the availability of both males and females on the bottom increases. Thus, by the time the males are ripe (October) the availability of redfish on the bottom is high. The mature male redfish cease feeding as the gonads ripen.

Feeding habits also have important effects on movements and distribution of redfish. Redfish feed off the bottom and the food consists almost entirely of deep-water animals. The dominant food for the sampled areas was the euphausiid *Meganyctiphanes norvegica*. Smaller catches of redfish at night are attributed to vertical movements. The movements are apparently a direct response to light changes, modified by a search for food. Redfish decrease in numbers with increasing depth between 100 to 175 fathoms (180 to 320 m.). This was related to the availability of *M. norvegica* which also decreases in numbers with increasing depth.

Redfish are primarily pelagic animals and the mature redfish of the Gulf of St. Lawrence must spend considerable periods off bottom. Light changes, feeding habits and the sexual cycle appear to be the major factors determining the pelagic and demersal distribution.

These findings serve to explain the diurnal and seasonal differences in the distribution and sizes of redfish available to the commercial fishery. They also emphasize the difficulties involved in sampling redfish populations for population studies.

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Further Study of the Influence of Short Storage Periods, 3 Days to 2 Weeks at 15°F., on the Quality of Frozen Cod Stored at 0°F.[1,2]

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ABSTRACT

Commercially frozen, packaged cod fillets subjected to 3-day, 1-week, and 2-week periods of storage at 15°F. (–9.4°C.) after storage at 0°F. (–18°C.) for 1 and 3 months, with subsequent storage at 0°F., underwent considerable deterioration in quality as measured by taste panel and protein solubility estimations. A 3-day period at 15°F. reduced the storage life by about 1½ months, a 1-week period by about 2 months, and a 2-week period by about 2 to 2½ months.

Previous experiments have shown that when packaged frozen cod fillets stored at 0°F. for a month or more were subjected to a 2-week exposure to 15°F., followed by subsequent storage at 0°F., they underwent considerable deterioration in quality (Dyer *et al.*, 1957). This was evident from measurements of taste panel grade and of protein extractability. As a further step in an investigation of the effect of a temporary rise in storage temperature on frozen fillets (as in an inadequately chilled refrigerator car), the effect of shorter exposures to the 15°F. temperature, for 3 days and 1 week as compared with 2 weeks, is reported in the present communication.

EXPERIMENTAL

Fillets of fresh cod iced for 2 days on the vessel were frozen and packed in master cartons holding twenty-four 1-lb. packages, as reported previously (Dyer *et al.*, 1957). Different lots of these cartons were then stored separately as follows:

I. Controls:
   A—stored continuously at 0°F.
   G—stored continuously at 15°F.
II. Stored for 1 month at 0°F., followed by:
   B—3-day exposure to 15°F., subsequent storage at 0°F.
   C—1-week exposure to 15°F., subsequent storage at 0°F.
   D—2-week exposure to 15°F., subsequent storage at 0°F.
III. Stored for 3 months at 0°F., followed by:
   E—3-day exposure to 15°F., subsequent storage at 0°F.
   F—1-week exposure to 15°F., subsequent storage at 0°F.

The temperature of the 0°F. storage box did not vary more than 0.4° from 0°C. over the storage period.

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[2]Paper No. 10 of a series "Proteins in Fish Muscle".

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Chemical analyses, including protein extractability and taste panel tests, were conducted every 3 weeks as previously reported (Dyer *et al.*, 1957).

RESULTS

The analytical results were similar to those obtained in the previous experiment: moisture, 81.7%; total nitrogen, 2.80%; non-protein nitrogen, 0.31%; "albumin" (water-soluble protein) nitrogen, 0.54%; trimethylamine, 1.1 mg. N per 100 g. tissue; trimethylamine oxide, 61.7 mg. N per 100 g. tissue. The protein nitrogen content was 2.49%, of which the albumin constituted 22%. During storage there was no change in any of these values.

Taste Panel Scores

The taste panel scores are shown in Fig. 1. Those of sample A, stored continuously at 0°F., dropped slightly faster than in the previous experiment, reaching the unacceptability level at about 6 months. Sample G, stored continuously at 15°F., lost its palatability very rapidly in the first month, becoming unacceptable at 1½ to 2 months.

Of the group II samples, preliminarily stored for 1 month at 0°F., Sample D, which received the 2-week exposure to 15°F., showed a drop in score of about 15 to 20% immediately after. Thus, the damage to the quality occurred within about the first week after the 15°F. exposure. On subsequent storage at 0°F., the grade diminished at the same rate as for sample A, but the keeping-time was reduced to about 4 months. (The term keeping-time, or storage life, is used here to indicate the storage time to the unacceptability level as measured by the taste panel.)

Sample C, given 1-week exposure to 15°F., behaved similarly to D, but the drop in grade, about 15%, was not quite as marked, the keeping-time being reduced to just over 4 months.

Sample B, which received the 3-day exposure to 15°F., was similarly affected; the grade decreased by 10 to 12%, at a little slower rate, which resulted in a keeping-time of about 4½ months.

For the group III samples E and F exposed to 15°F. after the 3-month storage at 0°F., the rapid decreases in taste panel grade were of substantially the same magnitudes as for B and C.

These results show that under the conditions used, the effect of shorter exposures to 15°F., 3 days and 1 week as compared with the 2-week period used in the experiments previously reported, is almost as detrimental to the quality of the frozen fillets.

Extractable Protein

Protein extractability, expressed as extracted actomyosin in percentage of total protein, is shown in Fig. 2. These results confirm the conclusions from the taste panel tests. The decrease in extractability was very rapid upon exposure to 15°F.

Of the group II samples, stored for 1 month at 0°F., D exposed for 2 weeks to 15°F. developed the largest decrease in protein extractability, C exposed

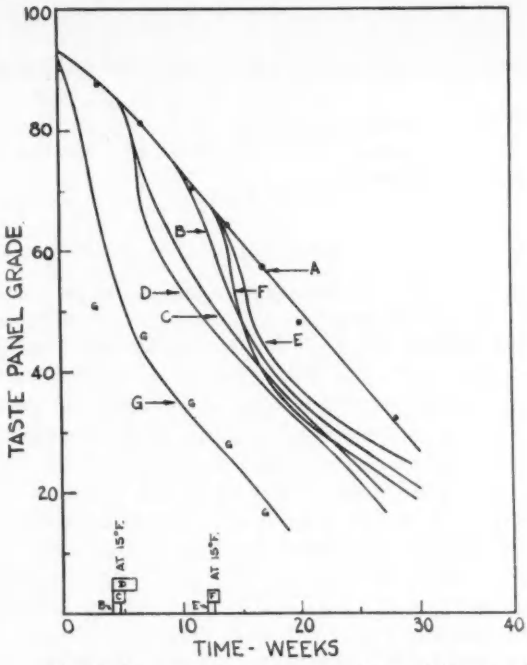

FIG. 1. Average taste panel grade in stored frozen cod fillets.

A—● Stored continuously at 0°F. (—18°C.)

B—Stored at 0°F. for 1 month, then 3 days at 15°F. (—9.4°C.), and subsequently at 0°F.

C—Stored at 0°F. for 1 month, then 1 week at 15°F., and subsequently at 0°F.

D—Stored at 0°F. for 1 month, then 2 weeks at 15°F., and subsequently at 0°F.

E—Stored at 0°F. for 3 months, then 3 days at 15°F., and subsequently at 0°F.

F—Stored at 0°F. for 3 months, then 1 week at 15°F., and subsequently at 0°F.

G—G—Stored continuously at 15°F.

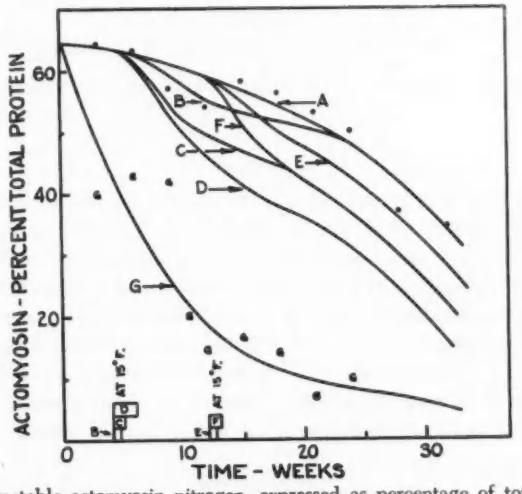

FIG. 2. Extractable actomyosin nitrogen, expressed as percentage of total protein nitrogen (2.49%), in stored frozen cod fillets. (Legend as in Fig. 1.)

for 1 week developed somewhat less, while B exposed for 3 days showed the least decrease.

For the group III samples exposed to 15°F. after 3 months at 0°F., the effect on E was about one-third of that observed for D, while the effect on F was about the same as that found with C.

DISCUSSION

Though it is known that the temperature of at least part of the load in an overhead-bunker refrigerator car may rise to 15°F. or higher during transcontinental runs in summer weather (Taylor and Harrison, 1948; Kelsey, 1956), the total time during which the frozen fish is at above 0°F. is not readily ascertainable. The total period is influenced by handling and storage conditions upon arrival at inland cold storages. Reliable data on these conditions are needed to assess their effect on the quality of the frozen fish. The contribution of transportation in overhead-bunker refrigerator cars to loss of quality is clear. The present results show that for periods of 3 days to 2 weeks, there is a very definite deterioration in quality under conditions simulating such refrigerator car transportation. This results in a loss of 2 to 3 months of the at least 6 to 8 months' storage life that can be normally expected for commercially frozen cod fillets stored continuously at 0°F. It must also be pointed out that considerable decrease in quality has occurred before the unacceptability level is reached; thus, even with shipment after only 1 month's storage at the coast, the quality of the frozen fillets reaching the market may have deteriorated significantly due to too high refrigerator car temperature.

The present data on the approximate storage life to unacceptability of rapidly frozen cod fillets, adequately packaged to prevent desiccation, may be summarized as follows:

At 15°F., 1½ to 2 months.
At 10°F., 3½ to 4 months (Dyer, 1951).
At 0°F., 6 to 8 months.
At −10°F., 9 to 10 months (Dyer, 1951).

These times are considerably less than those suggested by Nicol and Lawrence (1956).

SUMMARY

The results of the previous work have been extended to include the effect of short storage periods of 3 days, 1 week, and 2 weeks at 15°F. on frozen packaged cod fillets stored previously and subsequently at 0°F. Significant deterioration, as measured by taste panels and protein extractability, occurred as a result of these treatments, and the longer the storage period at 15°F., the greater was the deterioration. The effect was the same with 3 months' previous storage at 0°F. as with 1 month. A 2-week storage period at 15°F. reduced the storage life by 2 to 2½ months, a 1-week period by about 2 months, and a 3-day period by about 1½ months. Significant deterioration has, of course, occurred before

these limits are reached. The effects were much the same whether the preliminary storage period at 0°F. was for 1 or 3 months.

Continuous storage at 15°F. led to very rapid deterioration.

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A New Technique for Studying Non-tidal Drift with Results of Experiments off Gay Head, Mass., and in the Bay of Fundy[1]

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ABSTRACT

A transponding drift buoy has been developed to aid in the study of the horizontal motions of surface waters. Experiments to study the non-tidal drift off Martha's Vineyard, Mass., in June 1956, off Yarmouth, N.S., in October and November 1956, in Grand Manan Channel in October 1956, and off Saint John, N.B., in December 1956, are described and discussed.

INTRODUCTION

The drift of a body of water and/or the planktonic forms contained therein has been the concern of the fishery biologist for a long time. The need for knowledge of the direction and speed of drift from the spawning ground, together with the eventual location of fish larvae when they cease their planktonic existence, has prompted many attempts to deduce the non-tidal drift in many parts of the sea.

One of the commonest techniques has been to broadcast drift bottles over the area of interest with the hope of recovering a sufficient number of them within a limited elapsed time to allow the construction of a map of the probable drift of these bottles with respect to both routes and speeds. The chief criticisms of this method have been that:

(a) The bottles may be subject to considerably more wind influence than the upper 5 or 10 m. of water in which the planktonic elements reside.

(b) Knowledge of only the point and time of release and the point and time of recovery leaves the assumed intervening route of each bottle entirely up to the deductions of the investigator.

(c) The elapsed time between stranding and discovery of the drift bottle or the possible temporary stranding at some other location prior to the final stranding and discovery, adds to the uncertainty of the rates of drift.

We have succeeded, we believe, in building and using a better drift bottle which we have called a "Transponding Drift Buoy". This buoy is not as elaborate as Stommel's (1954) nor as simple as that of Volkmann, Knauss and Vine (1956). It could readily be adapted for use with a parachute drogue for studying subsurface ocean currents after the method of Volkmann *et al.*

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Brief Description of Transponding Drift Buoy

Each buoy is 20 feet long, 6 inches in diameter, constructed of aluminum, loaded with a radio transmitter and receiver and a battery stack (Walden, Ketchum and Frantz, 1957) and ballasted with lead. The buoy floats vertically with 2 feet of freeboard surmounted with a 13-foot whip antenna. Total weight in air is 230 lb. A 4-foot-diameter disc of plywood, painted orange and bearing an identifying letter, is tethered to each buoy to improve visual identification from the air.

When the receiver is energized by a short, 1- to 2-sec. tone-modulated signal on 2398 kc., the transmitter responds with CW signals on 2398 kc. of 15 sec. duration. This signal may be DF'd by ship or aircraft. Repetitions of this procedure and suitable manoeuvring of the ship or aircraft will bring the target buoy within visual range where a fix may be made either by loran, cross bearings on objects of known positions, or whatever other method is suitable.

The expected life of the power supply in each buoy under normal tracking conditions, i.e., located once per day, is 2 to 3 weeks.

In the experiments described below, two cases of buoy failure can be definitely attributed to the antenna breaking in rough weather. It is reasonable to attribute the loss of the three still missing buoys to similar troubles. Steps currently being taken to remedy this fault and other minor ones which we have been able to isolate should add greatly to buoy efficiency.

Since the buoys used in these experiments are intended to follow the movement of the upper 5 m. of water, they are ballasted to make the normal freeboard as little as possible consistent with reliable radio transmission in a seaway, thus mimimizing the direct effect of windage. A rough calculation, based on only the relative areas exposed to air and water, shows the buoy to move in still water at approximately one-sixtieth the wind velocity, a motion which is negligible relative to the other inaccuracies of these experiments. In the presence of steep waves, the motion is surely somewhat greater than this, because of the frictional motion of the surface layers and because of the actual transport due to the wave motion. But until we have more knowledge of actual velocity profiles near the surface under various conditions of wind, sea and temperature, we feel justified in assuming that the motion of these buoys indeed represents the data sought, the average horizontal velocity of the upper 5 m. of water.

EXPERIMENTS

Five sets of experiments have been performed with these buoys:

A. A trial test of the development model southwest of Gay Head, Martha's Vineyard, Mass., in June 1956.

B. An experiment in the Lurcher Shoals–Trinity Ledge area off Yarmouth, N.S., in October 1956 with one buoy.

C. An experiment in Grand Manan Channel in October 1956 with three buoys.

D. An experiment in the Lurcher Shoals–Trinity Ledge area off Yarmouth in November 1956 with six buoys.

E. An experiment off Saint John, N.B., in December 1956 with four buoys.

The experiments in Fundian waters were conducted at the invitation of the Fisheries Research Board of Canada Biological Station, St. Andrews, N.B., as a part of their joint Fisheries Research Board of Canada–U.S. Fish and Wildlife Service herring investigations. These drift buoy experiments were sandwiched in between a series of cruises by two vessels, *Harengus* and *Silver Bay*, to discover where young herring are produced and where they drift during the first few months after hatching. These distribution and dispersal cruises traversed the Bay of Fundy, the Gulf of Maine and Georges Bank. Regular drift bottles were set out at frequent intervals along the ships' tracks on these cruises. The over-all picture, as deduced from their pattern of returns, will be the subject of another paper. Drift bottles were also set out with each of the transponding drift buoys.

EXPERIMENT A

On 11 June, one transponding drift buoy was set adrift 30 miles WSW. off Gay Head, Martha's Vineyard. During the following 2 weeks the position of the buoy was determined as often as weather conditions and other commitments of our aircraft permitted. The buoy was located six times (Fig. 1). It was last located within 7 (nautical) miles of its initial position, but in the course of 2 weeks had drifted throughout at least one clockwise orbit, having been 18 miles to the ESE. and 21 miles to the WSW. of the initial position. The buoy responded at 1345 on 26 June while our boat *Asterias* was en route to recover it but failed to respond at 1430 and at frequent triggerings thereafter. We eventually learned that a tug with a tow had wiped off the antenna at 1420 on the same date. The buoy was picked up by a U.S. Navy destroyer escort and returned to us otherwise undamaged.

The indicated rates of drift of this buoy are of interest. Following a relatively slow northward drift on the first day the buoy moved southeasterly at a rate of 15 miles per day, then westerly and southwesterly at decreasing rates. During the last week, with fixes on 18 and 25 June, the drift was NNE. at only 2 miles per day. It is possible that had fixes been made more often during the last week the rates of drift would have been larger, for we have no reason to believe, on the basis of its drift during the previous week, that it went directly to its last observed position.

Conventional drift bottles set out by the U.S. Fish and Wildlife Service vessel *Albatross III* (Cruise 76) on 11 and 23 June in this area moved northward into coastal waters in about a month, or with an average non-tidal drift of 1+ miles per day.

This first experiment with the transponding drift buoy suggests that prior to the eventual northward set these waters underwent an anticyclonic irrotational motion, one erratic in its rates of movement and direction, suddenly speeding up and gradually slowing down. It may have been repeated several times as these waters drifted shoreward.

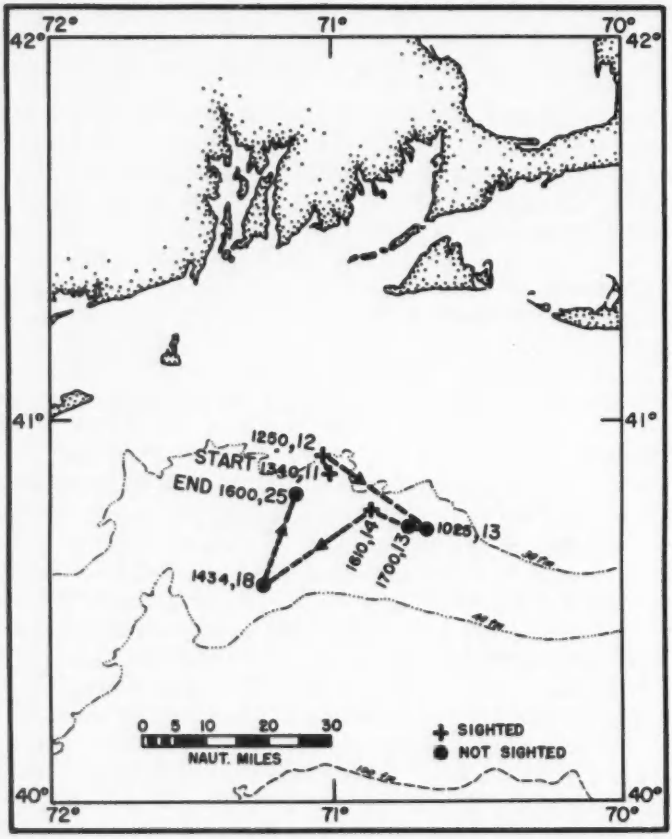

FIG. 1. Experiment A, June 1956, SW. of Gay Head, Mass. Numbers indicate time (EDST) and date of buoy location.

EXPERIMENT B

It was our intent for the first experiment in the Bay of Fundy to set out several buoys in the Lurcher Shoals–Trinity Ledge region (an area considered to be one of the major herring spawning grounds) and to allow them to drift for the first 2 weeks of October. As is commonly the case with newly developed electronic equipment, we were troubled with failures. We did succeed, however, in tracking one buoy for a period of 6 days, 4–10 October 1956 (Fig. 2).

This buoy was launched at position "Y" halfway between Lurcher Shoals and Trinity Ledge. At the end of 5 days the buoy was in the mouth of Saint Mary Bay and on the afternoon of the sixth day it was off Digby Neck in the Bay of Fundy, about 43 miles from position "Y". One would presume that it went through Petite Passage, though it may have gone through Grand Passage

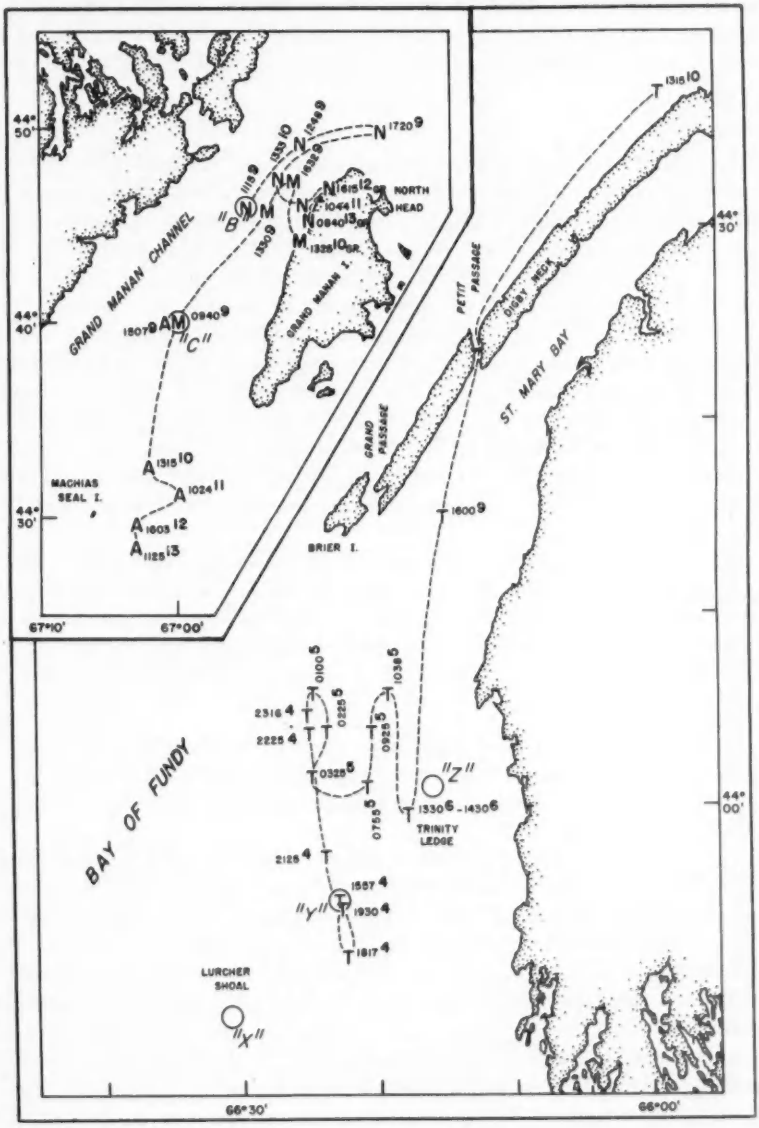

FIG. 2. *Lower*—Experiment B, October 1956, Lurcher Shoal–Trinity Ledge area.
Upper—Experiment C, October 1956, Grand Manan Channel.
Numbers indicate time (AST) and date of buoy location.

or even around Brier Island. Suffice it to say that the resultant non-tidal drift on that occasion was northerly at slightly greater than 7 miles per day. Except for a half a day of strong SE. wind the winds were light throughout the period of drift.

EXPERIMENT C

In order to facilitate repairs and experimenting, the field team shifted its scene of operation to the Grand Manan Channel, just a few hours steaming time from the Biological Station at St. Andrews. Here three buoys were set adrift and tracked for a period of 4 days, 9–13 October 1956 (Fig. 2, inset). The buoys were set out at Station "*C*" near the beginning of the flood, at Station "*B*" 1½ hours later, and at Station "*C*" at the beginning of the ebb.

The results of this experiment suggested that there is a tendency toward a non-tidal set onto the western shore of Grand Manan Island, superimposed on the large (8- to 9-mile) tidal excursion. The buoy at position "*C*" moved well up the channel on the flood and was found stranded on the western shore of Grand Manan the following afternoon. The buoy set out at "*B*" also moved northerly on the flood to a position NNE. of North Head, returned into Grand Manan Channel by the following afternoon, and stranded on the western shore of Grand Manan 2 days later.

On the other hand, the buoy launched at "*C*" at the beginning of the ebb moved southerly out of the area a distance of about 7 miles the first day, then more slowly on successive days to the vicinity of Machias Seal Island. The resultant drift after the buoy left the effect of the strong tidal excursions of the Grand Manan Channel was about a mile per day, southerly.

EXPERIMENT D

Owing to the large tidal excursions common in the Fundian region, we planned for this November experiment to set out the buoys at position "*X*", "*Y*" and "*Z*" (Fig. 3) at the beginning of the flood and at the beginning of the ebb, one-half tidal cycle apart.

The first string of buoys was set out near the beginning of the flood as planned, but due to electrical failures only two buoys were set out in the second string, at Stations "*Y*" and "*Z*", one and one-half tides later. A third setting was made several days later irrespective of the tidal phase (Fig. 3).

Buoy *Tango* (T), set out at "*X*" on 2 November, moved northwesterly for 1¼ days at a rate of about 17 miles per day and then failed to respond and remained lost.

Buoy *India* (I), set out on 2 November at "*Y*", also failed to respond, was sighted by the vessel *Silver Bay* at Northwest Ledge off Brier Island on the 7th, and henceforth remained lost. It had moved to its last seen position at better than 4 miles per day. The orange disc for this buoy was sighted a month later about 60 miles to the northeastward, 8 miles northeast of Parker Cove.

Buoy *Mike* (M), set out the same day at "*Z*", moved southwesterly, northwesterly, southerly, then northerly into the Bay of Fundy, the final resultant being about 4 miles per day.

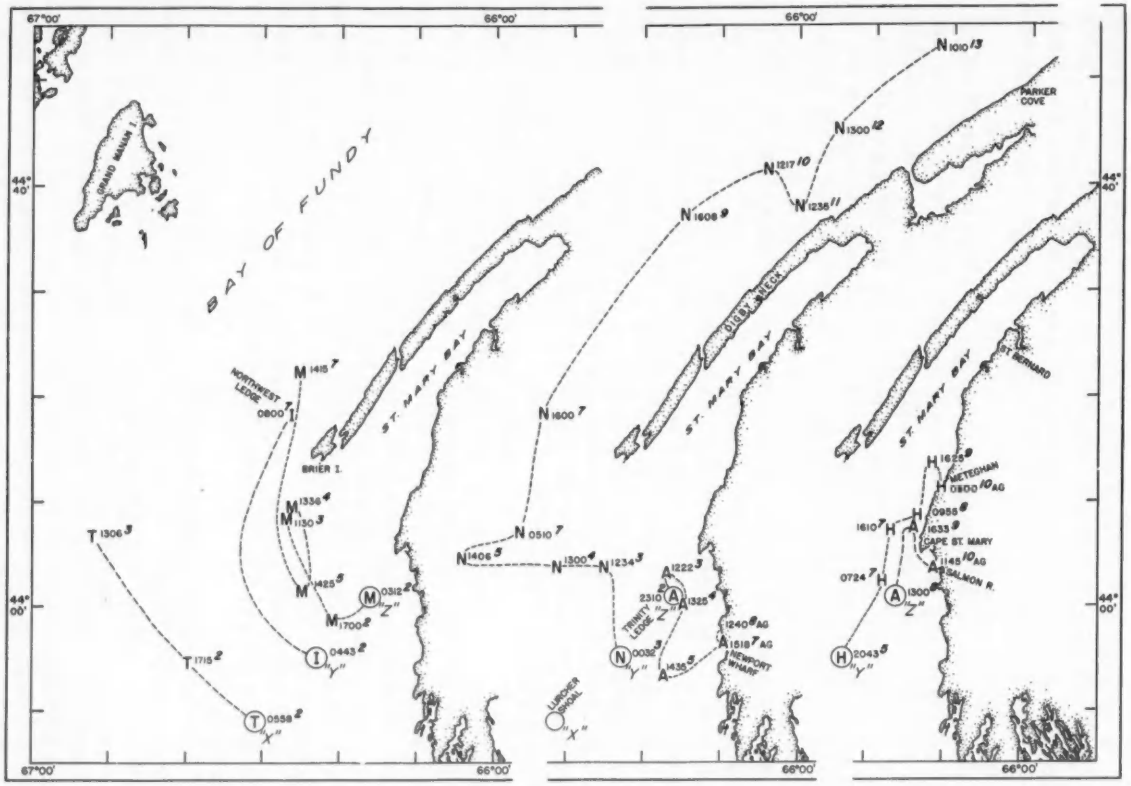

FIG. 3. Experiment D. November 1956, Lurcher Shoal–Trinity Ledge Area. Part I–left, Part II–centre, Part III–right. Numbers indicate time (AST) and date of buoy location.

The second string of buoys was set out near midnight of 2–3 November. Buoy *November* (N) at "Y" moved northerly, westerly and then northeasterly at 4 to 16 miles per day with a resultant when picked up 10 days later off Parker Cove of 7.5 miles per day. On the other hand, Buoy *Alpha* (A), set out at "Z", moved northerly, then southerly and easterly at much slower rates, 3 to 7 miles per day, and stranded off Newport Wharf on 7 November only 7 miles from Trinity Ledge.

The third part of this experiment was begun by setting out Buoy *Hotel* (H) at "Y" on the evening of 5 November and by resetting *Alpha* at "Z" near noon on the 8th. *Hotel* moved northerly past Cape St. Mary into the mouth of St. Mary Bay at about 5 miles per day, then southerly during the latter part of the 9th to strand at Meteghan. *Alpha* moved northerly past Cape St. Mary on the 8th and 9th at about the same rate as *Hotel*, then southerly as did *Hotel*, to strand near the mouth of Salmon River.

It is apparent that there is no set pattern of drift away from the Lurcher Shoals–Trinity Ledge area which is repetitive day after day. The first string of buoys set out in November exhibited a decided offshore drift during the first day, followed by a northwesterly drift, possibly a reversal on 4 and 5 November as indicated by *Mike*, and then a northerly drift out of the area into the Bay of Fundy proper. This suggests very strongly a wind influence superimposed on the non-tidal drift. The winds were fresh northeasterly on the 2nd and 3rd, fresh northerly on the 4th and 5th, followed by westerlies and southwesterlies (see accompanying Table). This is further indicated by the drift of Buoys *November* and *Alpha* in Part II and *Hotel* and *Alpha* in Part III of the experiment. For instance, the tendency following the early morning of 2 November was offshore, westerly and then northerly out of the area. Following midnight on the 2nd, the tendency was northerly and westerly out of the middle of area "Y" but ultimately toward shore from Trinity Ledge ("Z"). After the 5th the tendency was northeasterly towards St. Mary Bay with a southeasterly reversal onshore on the 9th and 10th. One of the drift bottles set out with Buoy *Hotel* on the 5th at position "Y" was found 9 days later on the eastern shore of St. Mary Bay at St. Bernard, having continued its northeasterly drift into St. Mary Bay at a speed of 3.5 miles per day. A second bottle was found on the 28th near where *Hotel* came ashore.

These experiments suggest that while the general tendency for the non-tidal drift is northerly across this area at a relatively high speed, 5 to 10 miles per day, there can be broad dispersion of fish eggs and larvae deposited in the water in the area due to the tendency of drift offshore, northerly, southerly or onshore, as modified by the wind pattern, in addition to the dispersion created by the regular tidal fluctuations.

It does seem, however, that the waters which drift across the Lurcher Shoal–Trinity Ledge area find their way into the Bay of Fundy in a relatively short time, 7 to 10 days, to off Digby with perhaps a small quantity of water being deflected into St. Mary Bay from time to time.

Surface winds in study areas as determined from U.S. Weather Bureau surface maps.

Date, 1956	Average wind	
	Direction	Force
	Lurcher Shoals area	
Oct.		
4	W.	3
5	NW.	3
6	E.	3
7	SW.	3
8	WSW.	4
9	WNW.	4
10	WNW.	3
	Grand Manan Channel	
Oct.		
9	WNW.	3
10	WNW.	3
11	WNW.	3
12	W.	2
13	W.	1
	Lurcher Shoals area	
Nov.		
2	NNE.	4
3	N.	3
4	N.	4
5	N.	4
6	NNW.	3
7	SW.	3
8	SW.	2
9	NW.	4
10	NNW.	5
11	SW.	3
12	SSW.	5
13	NW.	4
	Bay of Fundy	
Dec.		
4	NW.	5
5	NE.	1
6	SSE.	3
7	W.	3
8	N.	3
9	NNE.	4
10	Variable	
11	SSW.	4
12	W.	5
13	ENE.	3
14	ENE.	4

Experiment E

The experiment in December was shifted to the area off Saint John, N.B., in order to avoid fouling the myriad lobster pot buoys and lines attendant to the opening of the lobster fishing season which commenced on 1 December. Only four buoys were available for this experiment (Fig. 4) inasmuch as *Tango* and *India* remained unreported. The experiment commenced on the 4th. Minor troubles were experienced and corrected until the night of 11–12 December when

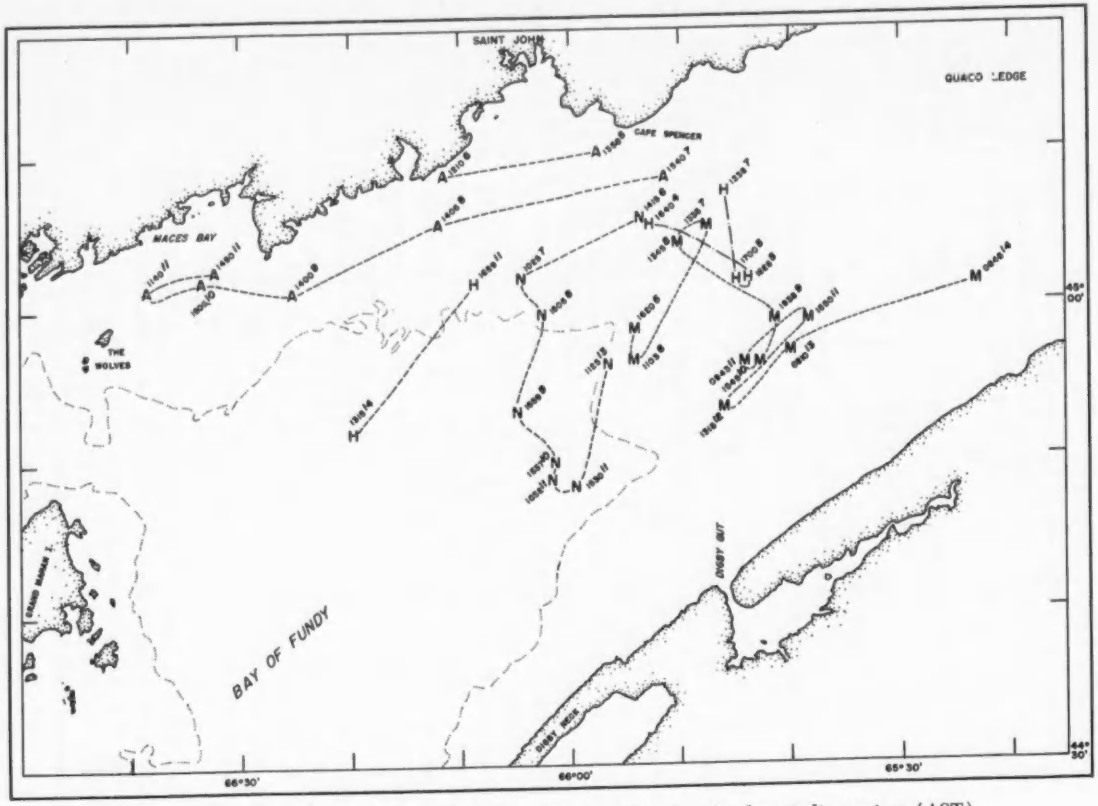

FIG. 4. Experiment E. December 1956, Central Bay of Fundy. Numbers indicate time (AST) and date of buoy location.

three of the buoys (*Alpha, Hotel* and *November*) lost their antennae in a storm. Two of these three (*Hotel* and *November*) were recovered, the vessel *Harengus* being conned to their location by the aircraft which was able to trigger the buoys from a distance of about 2 miles in spite of the absence of the antennae. The third buoy (*Alpha*) had not been recovered by the end of the experiment.

Buoy *Alpha* had been set out 2 miles southwest of Cape Spencer on 5 December and drifted westerly to less than a mile offshore at a speed of 10 miles per day. This buoy was picked up and relocated farther offshore on the 7th. It again drifted westerly at high speeds to the offing of Maces Bay where it stagnated. *Alpha* was not located again following the afternoon of the 11th until late in December when it was sighted by a lobsterman on Muir Ledges south of Grand Manan. The presumption is that its antenna was broken off in the storm referred to above.

Buoy *Hotel*, set out 7 miles south of Cape Spencer on 4 December, drifted 7.5 miles southeasterly, then northerly where it was picked up for repairs on the 7th.

Buoy *November*, set out 6 miles south of Cape Spencer on 6 December near *Hotel*, moved westerly at a fairly high speed until the 7th, then veered southerly at speeds averaging 3+ miles per day, then northeasterly.

Buoy *Hotel*, set out on 11 December just west of where *November* veered southerly, was found 3 days later 12 miles to the southwest.

Buoy *Mike*, set out farther offshore 13 miles south of Cape Spencer on 5 December, underwent a series of irregular courses until at the end of 7 days it was oscillating forth and back just outside the easterly flowing current on the southeast side of the bay. On the 12th, *Mike* became entrained in the easterly current and had drifted 18 miles to the eastward by the morning of the 14th.

Buoy *Hotel* was also allowed to drift for a period of two days (9–11 December) in the area about 12 miles south of Cape Spencer (not figured) in which it described an arc to the south and east, moving at about 3 miles per day.

This experiment has revealed several things of interest, namely:

(a) The width of the westerly flowing non-tidal drift on the northwest side of the bay; the width of the easterly flowing non-tidal drift on the southeast side of the bay; and the irregular cyclonic eddying motion in the central portion of the Bay of Fundy between the coastal drifts.

(b) It is apparent that the westerly drift along the New Brunswick coast extends to a distance of about 6 miles south of Cape Spencer. Note that *Hotel*, launched at this distance from the Cape on the 4th, drifted southeasterly out of this flow but that *November*, launched on the 6th, remained in it until the following morning when it veered southerly out of the drift. This drift appears to have a speed of the order of 10 to 15 miles per day.

(c) The easterly coastal drift on the southwest side of the bay appears to be about 10 miles wide, opposite Cape Spencer. Note that Buoy *November* had been carried by this drift one month before to a position just south of where *Mike* performed the hesitation waltz on the 9th to 12th prior to being entrained in the coastal drift.

(d) The apparent irregular wanderings of Buoys *Hotel, November,* and *Mike* are suggestive of cyclonic motions in the central part of the bay lying between and contiguous to the west-moving and east-moving coastal currents.

(e) The non-tidal drifts did not appear to be as much affected by wind in this area as they had been in the Lurcher Shoal–Trinity ledge area. In several instances adjacent buoys in the centre of the bay moved in opposite directions during periods of high wind force.

Obviously it would have been desirable in these experiments to have established each buoy position at the same state of the tide, in order to minimize the periodic excursions due to tidal currents alone. It soon became apparent that this was impossible because of the generally poor flying weather and the shortness of the daylight hours at this time of year. However, an attempt was made to correct the positions of Buoys *Mike* and *November* in this last experiment to the nearest time of high water at St. John on the basis of published data (Canada, 1928). These buoys drifted in an area fairly close to Station A, 44° 58.5′ N., 65° 57.0′ W., of the survey made in 1907 of the tidal currents in the Bay of Fundy by the Canadian Hydrographic Service. These corrections were made by integrating the published hourly current vectors at the station and correcting the resultant displacements for the difference of the actual range of tide at Saint John and the 21-foot range of the tables. The results were somewhat inconclusive. There was, perhaps, a tendency to smooth out the trajectory of Buoy *November,* and the apparently random initial excursions of Buoy *Mike* assumed a more definitely counterclockwise appearance; but application of the correction would not warrant a change in interpretation of the data. Since these tidal data were available in only one location in the area of this experiment, and since our justification for using them even a few miles from the original current stations is questionable, we have not attempted to apply tidal corrections to the observed positions.

CONCLUSION

These experiments have added some detail to the general description of the circulation in the Bay of Fundy as summarized by Ketchum and Keen (1953, pp. 98–99) and have confirmed the existence of the same general pattern for the late autumn period, there being no previous drift experiments at this time of year in this region. The inflowing drift, restricted to the southeasterly side of the bay, averages about 10 miles per day, and the outflowing drift is restricted to the northwest side at comparable speeds. The inflowing drift is about 10 miles wide off Digby and the outflowing drift is about 6 miles wide off Cape Spencer. While some trajectories from the Lurcher Shoal–Trinity Ledge region may penetrate well up the bay, perhaps even to its head, the cyclonic rotations with speeds of 2 to 4 miles per day between the two drifts may shorten the route and provide for the distribution of herring larvae all along the New Brunswick coast, beginning about 15 to 20 days after hatching. Because of the streakiness of the

drift, these planktonic elements may become considerably dispersed and take much longer to arrive.

The above time agrees with that of Fish and Johnson (1937, p. 200) but we postulate higher speeds along the periphery and slower ones in the central eddying motions, and possible deeper penetration into the bay along the southeast side prior to crossing over to the other shore. Mavor (1922), Fish and Johnson (1937) and Hachey and Bailey (1953) have tended to restrict the routes of drift bottles reaching the New Brunswick shore to the vicinity of the 50-fathom contour. However, many drift bottles have penetrated to the eastern end of the bay at all seasons of the year (Bigelow, 1927; Hachey and Bailey, 1952; Day, 1957). We believe that the transfer from the inflowing to the outflowing drift can take place all along the centre portion well up into the bay. Further experiments comparable to those we have reported above will be required to demonstrate this.

We have not added much to an understanding of the circulation around Grand Manan. We must agree with the conclusion of MacGregor and McLellan (1951) that the residual current in Grand Manan Channel may be variable depending upon tidal range and meteorological conditions.

ACKNOWLEDGMENTS

The transponding drift buoy was designed and developed under Contract Nonr-769(00) with the U.S. Office of Naval Research by Messrs. Walden, Ketchum and Frantz. The aircraft was made available through the same contract. The six buoys were constructed and the field work was carried out under Contract No. 14-19-008-2377 with U.S. Fish and Wildlife Service. The assistance of the Fisheries Research Board of Canada Biological Station at St. Andrews, in particular through Mr. S. N. Tibbo, is gratefully acknowledged as are the services of the Canadian Department of Fisheries vessel *Harengus*, Capt. L. J. Lewis, Master. We are also indebted to the crew of the PBY aircraft, Capt. Norman Gingrass, together with the scientific observers who assisted in the field work. Thanks are due to Messrs. Dingwell, Chute, Barstow and Wing for their efforts in construction and repair of the instruments, and to Mr. G. Pasley for preparing the Figures.

The Canadian Department of Transport kindly permitted the experiment to be carried out in waters under its jurisdiction. The U.S. Coast Guard, through its Local Notice to Mariners, and the Canadian Broadcasting Corporation, through its 5 p.m. "Fisherman's Broadcast", kept mariners informed of the project and indirectly helped to recover some of the "lost" buoys. Mr. E. G. Sollows of the Fisheries Research Board, at Yarmouth, N.S., also rendered assistance through his contacts with the fishermen along the Nova Scotia coast.

We are also indebted to the Commanding Officer, Dow Air Force Base, Bangor, Me., and the Commanding Officer, Greenwood RCAF Base, N.S., for use of base facilities by the PBY aircraft and personnel.

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The Effect of the Prevailing Winds on the Inshore Water Masses of the Hecate Strait Region, B.C.[1]

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ABSTRACT

Observations show that during the winter period of strong southeast winds, light surface waters accumulate along the coast, displacing the deeper waters offshore. During the summer period of weak southeast winds the accumulated surface waters move offshore allowing the return of the deep waters.

The winter accumulation is accompanied by a northwestward-flowing coastal current which appears to be continuous from California to the Gulf of Alaska. During the summer this current is small or absent.

It is noted that this seasonal change of water masses accounts for a major part of the observed sea level oscillation.

It is suggested that the winter displacement of deep waters and their return affect the movement of bottom fish of the region.

Seven oceanographic surveys were carried out by the Pacific Oceanographic Group into the three coastal regions of Queen Charlotte Sound, Hecate Strait and Dixon Entrance during the year May 1954 to June 1955 (Fig. 1). Routine observations of salinity, temperature and dissolved oxygen were made at 75 positions on a planned grid during each survey. During the summer months hourly observations of currents were made at several depths, generally for periods of 50 hours, at selected positions. All of these data have been reported (Pacific Oceanographic Group, 1955a, b, c).

The data indicate that surface salinities are low, 30 to 32‰, over the entire area during all seasons. There is a gradient from oceanic salinities along the seaward side of the area to lesser values along the mainland shore. In Dixon Entrance, surface salinities are generally less than in either Hecate Strait or Queen Charlotte Sound. Dilution from land drainage and precipitation is evident in all seasons, particularly in the southeast and northeast sectors, and along the mainland coast.

The annual range of surface temperatures varied between 6°C. in April and 14°C. in August. No consistent gradient normal to the coast was observed. In general, the surface waters of Dixon Entrance were colder than the waters farther south.

The typical seasonal sequence of salinity and temperature in the inshore part of these coastal regions is illustrated by the observations made at Station 21 (Fig. 2). Considerable variation during the year was observed at all depths. That occurring in the surface layer (above 100 m.) would be expected; and is attributable, in part at least, to seasonal variations in the amounts of insolation and fresh water from land drainage and precipitation.

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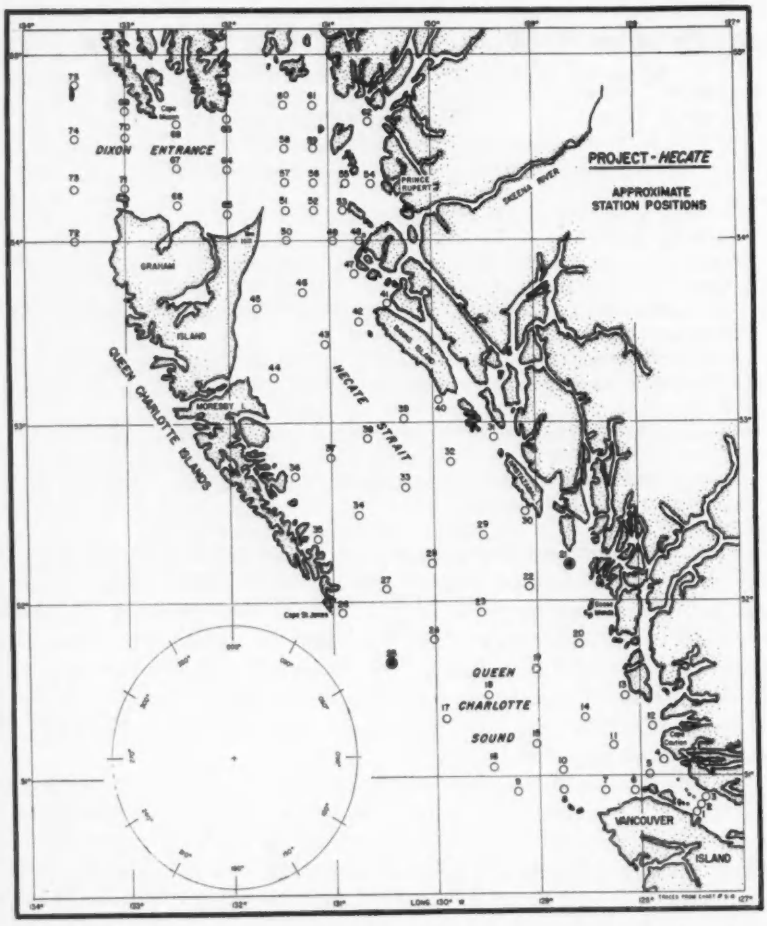

FIG. 1. Chart of the Hecate region showing the approximate position and number of the stations at which observations were made.

In the deep water there is a marked cyclic alternation of water masses. The alternation is between a summer and a winter water, the winter water being warmer and less saline than the summer water. This seasonal cycle of salinity and temperature of the deeper water is a marked feature of the data obtained on the Hecate surveys. The range of the seasonal variation was greatest along the mainland coast and became less with distance seaward.

While secondary factors such as topography may influence the extent of the variation in specific localities, the phenomenon is being ascribed principally to the onshore transport of surface water caused by the prevailing southeast winds in winter.

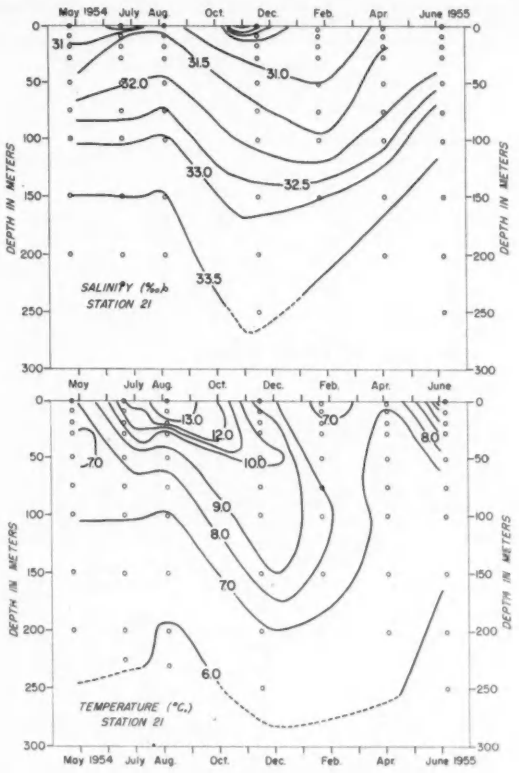

FIG. 2. Salinity and temperature observations at Station 21.

The seasonal sequence of southeast wind as observed at Prince Rupert (accompanying Table) indicates that they are strongest during the winter when, on the average, 4,000 to 5,000 miles of wind per month occur. During the summer an average of 1,000 miles per month has been recorded. In this inshore region it is apparent that the southeast winds are dominant throughout the year.

Under these wind conditions, surface water would be transported toward the coast (Fig. 3a). Close to the shore the water would move parallel to it and in the same sense as the wind. Thus there would be a region of convergence between the shoreward and alongshore movements (Sverdrup *et al.*, 1942). Between this convergence region and the shore the lighter of the transported surface waters would accumulate, causing an offshore displacement of the deeper water (Fig. 3b). In the spring, as the intensity of the southeast winds decreases, a relaxation of the onshore transport would occur. As a result, an offshore movement of the accumulated surface water and a compensating inshore movement of the deeper water would take place. The alternation of these

Summary of wind observations at Prince Rupert, B.C., indicating percentage frequency and average wind speed (Boughner and Thomas, 1948).

	January 1922 to December 1945											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Percentage frequency (by directions)												
North	13	15	16	12	11	11	10	9	13	13	13	16
Northeast	8	6	5	4	2	2	2	2	3	4	6	8
East	8	7	5	4	4	2	2	3	3	6	10	8
Southeast	42	40	42	40	35	26	27	30	31	47	44	44
South	4	4	4	6	8	8	10	12	10	5	4	3
Southwest	3	4	5	5	7	10	8	7	4	2	4	3
West	4	4	4	6	7	10	10	7	4	2	2	2
Northwest	7	8	9	12	12	12	11	10	12	8	6	6
Calm	11	12	10	11	14	19	20	20	20	13	11	10
Average wind speed in miles per hour (by directions)												
North	2.9	2.8	3.0	3.2	2.9	2.5	2.5	2.5	2.9	3.0	2.9	3.0
Northeast	4.2	5.3	4.0	4.2	3.5	2.2	2.2	2.9	4.0	3.9	4.1	4.1
East	9.1	6.7	10.2	6.9	5.8	2.7	3.5	3.9	6.1	10.2	11.7	9.5
Southeast	14.5	13.1	12.4	10.9	8.7	6.9	6.4	6.3	9.0	11.6	13.6	14.2
South	7.4	5.7	5.9	6.0	5.2	4.3	4.6	4.3	5.0	6.0	6.8	6.2
Southwest	5.0	5.9	5.7	5.2	3.9	3.6	3.6	3.3	3.7	4.2	6.2	6.7
West	3.1	3.0	4.4	4.2	3.6	4.0	3.7	3.1	2.9	2.6	2.9	2.8
Northwest	3.8	3.8	4.4	3.6	3.8	3.3	3.5	3.4	3.2	2.0	3.9	3.2

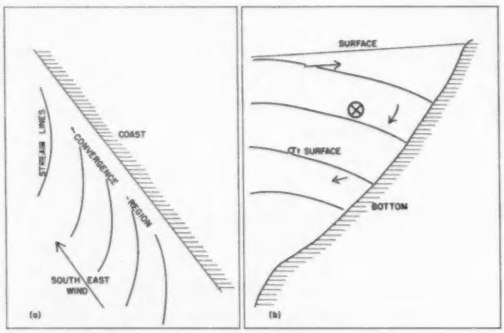

FIG. 3. (a) Surface water movement under the influence of southeast winds.
(b) Displacement of σ_t surfaces due to the accumulation of light water in a section normal to the coast. Tail of arrow indicates current direction.

processes results in the observed cycle. The winter accumulation of lighter water near the coast indicates a coastwise current in the same direction as the surface wind current.

An indication of the extent of this structure is allowed through a comparison of the observations made at Station 25 (Fig. 4) with those made at Station 21. At Station 25 the observed annual cycle of temperature and salinity

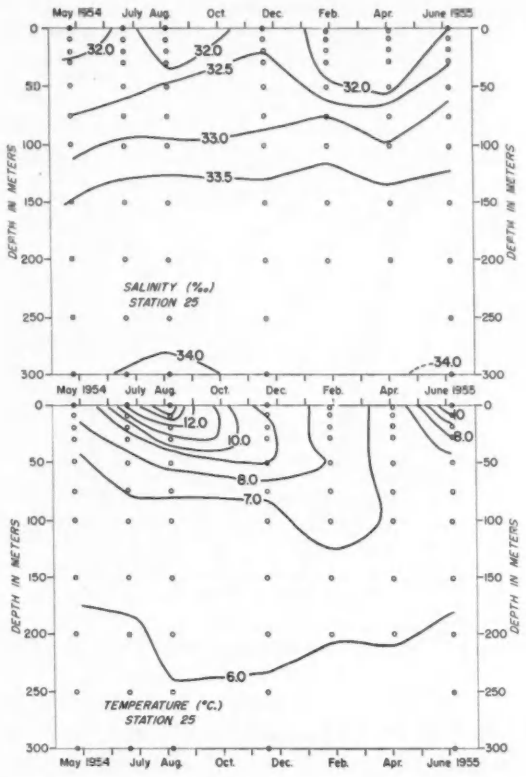

FIG. 4. Salinity and temperature observations at Station 25.

of the deeper water did not take place. Therefore it is reasoned that the water movement influencing the properties of the deep water at Station 21 did not occur at Station 25. Thus the data suggest a water movement from the southward, inshore of Station 25.

The observed distribution of density (σ_t) across Queen Charlotte Sound from Cape St. James to Triangle Island during December (Fig. 5) is further illustrative of the structure indicating this water movement. It is evident from a dynamic interpretation of these data that a strong movement into Queen Charlotte Sound was occurring between Station 25 and the northwestern end of Vancouver Island at this time. The data indicate, therefore, the existence of a winter water movement from the outer coast of Vancouver Island into Queen Charlotte Sound.

The structure in this section during the period of minimum southeast winds in the summer is shown in Figure 6. This suggests that the summer coastwise

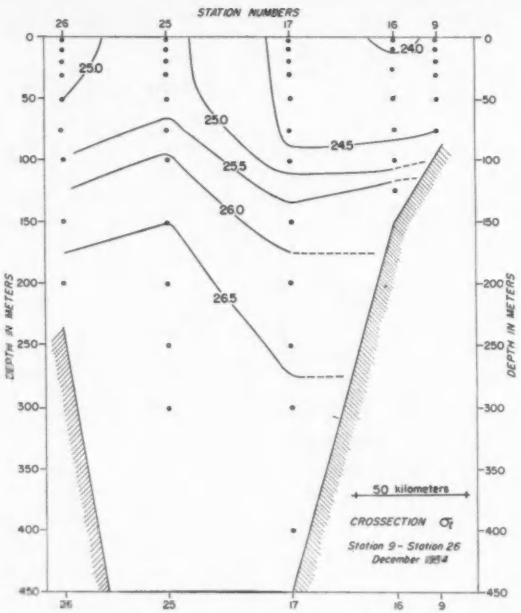

FIG. 5. Density (σ_t) distribution, Station 9 to Station 26 in December 1954.

current is small. Direct observations during the summer (Barber, 1956a) found no net movements greater than 5 miles per day (10 cm./sec.). Evidently, therefore, the inshore current fluctuates seasonally as defined by the structure, and since the seasonal variation of structure occurred over most of the region, it may be assumed that the consequent coastal water movement is a principal feature of the winter oceanography.

Since the accumulation of low salinity water along the coast persists apparently throughout the winter, the question of availability of such a water farther to the south is immediately evident. The work of Marmer (1926) and Tully (1938), the drift experiments of the International Pacific Halibut Commission (Thompson and Van Cleve, 1936), and observations discussed in the Canadian Hydrographic Service (1954–1955) Pacific Coast Tide and Current Tables provide ample evidence to show that in winter a predominant surface water movement to the northwest, close to the coast, occurs from California to the Gulf of Alaska. The present data show that this movement must be associated with accumulation of light water along the coast. It is suggested that the summer runoff from the Fraser and Columbia Rivers probably accumulates in the sea near their outflows until the occurrence of the autumn southeast winds, and then moves northward along the coast.

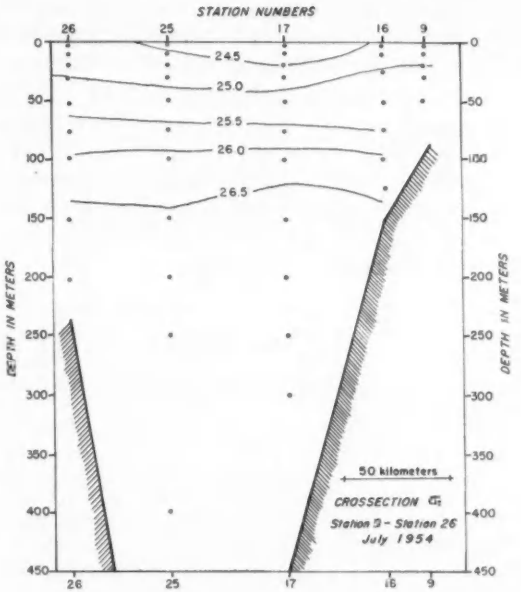

FIG. 6. Density (σ_t) distribution, Station 9 to Station 2 in July 1954.

A number of interesting considerations are manifest.

First, it has been shown that a similar seasonal sequence of salinity and temperature occurs in Queen Charlotte Strait (Barber, 1956b) and may be expected in other such inshore areas.

The second consideration concerns the effect of the less dense winter water on the height of sea level along the coast. The winter–summer difference of height calculated from the salinity and temperature observations at Station 21 in December 1954 and June 1955 was 26 cm. The seasonal variation of atmospheric pressure would lead to a sea level difference of approximately 5 cm. (Patullo *et al.*, 1955). Combined, they would produce a sea level difference of 31 cm. Mean monthly sea level data observed at Prince Rupert by the Canadian Hydrographic Service indicate that sea level differed by 34.3 cm. between December and June. Therefore it may be suggested that the alternation of water masses is responsible for a large part of the observed sea level oscillation.

The combination of wind and sea level data suggests that variations in the transport during the winter may occur. In January 1950, for example, little southeast winds occurred and mean sea level was about 24 cm. lower than normal. The suggestion is that during this month the warmer, less saline water at depth would not have been observed. It is possible that the observations of mean sea level would provide an index to the occurrence of these phenomena.

Third, it is suggested that this general mechanism which brings about in winter a warm, deep water may be of importance to the survival of bottom-feeding fish of the region. A cyclic alternation of the depth of lemon sole and brill has been noted (Barraclough, 1954; Ketchen, 1956). The association of the movement to deeper water and the winter accumulation is striking. While factors other than temperature may be important, they are probably coincident variables. Therefore the temperature may be an indicator of this movement. If so, it would be of value to encourage observations of the temperatures on the grounds in these areas when fishing; such observations have proven pertinent to fishing efforts in many other fishing areas of the world.

ACKNOWLEDGMENT

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Results from Tagging Experiments on a Spawning Stock of Petrale Sole, *Eopsetta jordani* (Lockington)[1]

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ABSTRACT

A review is made of the historical development of the petrale sole (*Eopsetta jordani*) fishery off the State of Washington (U.S.A.) and British Columbia (Canada), with statistical records of catches. A shift in recent years in the depth of trawl fishing from shallow water over the continental shelf to deeper water on the continental slope resulted in the discovery of dense concentrations of petrale sole at depths from 170–250 fathoms off the west coast of Vancouver Island. Tagging was carried out in the early spring of 1954 and 1955 on these deep-water stocks. Recoveries to May 30, 1956, from some 3,800 tags released showed that the male segment of the stock moved north and inshore along the Vancouver Island coast after spawning and at least part of the stock moved eventually into Hecate Strait, British Columbia. The tagged population contributed mainly to the fisheries adjacent to the northwest coast of Vancouver Island and in the Queen Charlotte Sound area. Subsequent recoveries from the Esteban Deep during the spawning seasons of 1955 and 1956 and the absence of the stock on this ground at other seasons, strongly suggest a homing tendency for this species. A discussion is given of the possible directive factors in the spawning migration. However, at the present time the actual factors involved remain unknown.

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INTRODUCTION

The petrale sole, usually called "brill" by Canadian fishermen, occurs along the western coast of North America. There is a commercial fishery for it at various places from Santa Barbara, California, to northern Hecate Strait, British Columbia. The method of catching is almost exclusively by otter-trawling gear. Along the California, Oregon and Washington coasts the fishery is prosecuted

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entirely by United States vessels, while off the British Columbia coast, vessels participating are from both Canada and the United States (mostly the State of Washington). The main fishing grounds for petrale sole, in waters adjacent to the Washington and British Columbia coasts, are illustrated in Figure 1.

HISTORY OF THE FISHERY

The history of the petrale sole fishery may be divided into two parts—the early development and expansion of the fishery on the shallow banks within the confines of the continental shelf, and the recent extension of fishing to deep water on certain parts of the continental slope.

Shallow Water Phase

Vessels from the State of Washington were the first to exploit stocks of bottom fish on banks along the exposed parts of the Washington and British Columbia coasts. The fishery for petrale sole began in the late nineteen twenties between Cape Flattery and Destruction Island, but remained unimportant until the late 1930's (Cleaver, 1949).

Between 1935 and 1942 the area of operation expanded gradually to include the Swiftsure and La Perouse Banks (40-mile Bank) and other banks along the west coast of Vancouver Island, as far north as Sydney Inlet. Detailed information on this early phase of the fishery is not available, and statistical data as to the composition and area of catches are incomplete.

Until about 1938, Canadian trawlers confined their activities to territorial waters of the Strait of Georgia in pursuit of species other than petrale sole. Between 1938 and 1942 there was a gradual expansion of this fleet to grounds along the lower west coast of Vancouver Island.

With the discovery of a high vitamin potency in dogfish liver and the rapid development of a market for food fish during World War II, there was a great expansion of both the Canadian and United States trawler fleets. The fishery expanded northward along the west coast of Vancouver Island and by 1944–45 vessels of both countries were exploiting grounds in Queen Charlotte Sound and Hecate Strait.

Between 1945 and 1953 the fishery for petrale sole underwent still further expansion to include all important banks along the British Columbia coast. However, these operations were largely confined to depths less than 100 fathoms, with best catches being made usually between depths of 40 and 70 fathoms. Canadian vessels, being of smaller size than their Washington counterparts, and being able to fish in the territorial waters of the British Columbia coast, have in general tended to operate in somewhat shallower water.

Deep Water Phase

Following 1950 the development of markets for a deep-water rockfish, the Pacific Ocean "perch", *Sebastodes alutus*, created an incentive for deep-water fishing. In a few years fishing operations were extended to 200 fathoms. This led

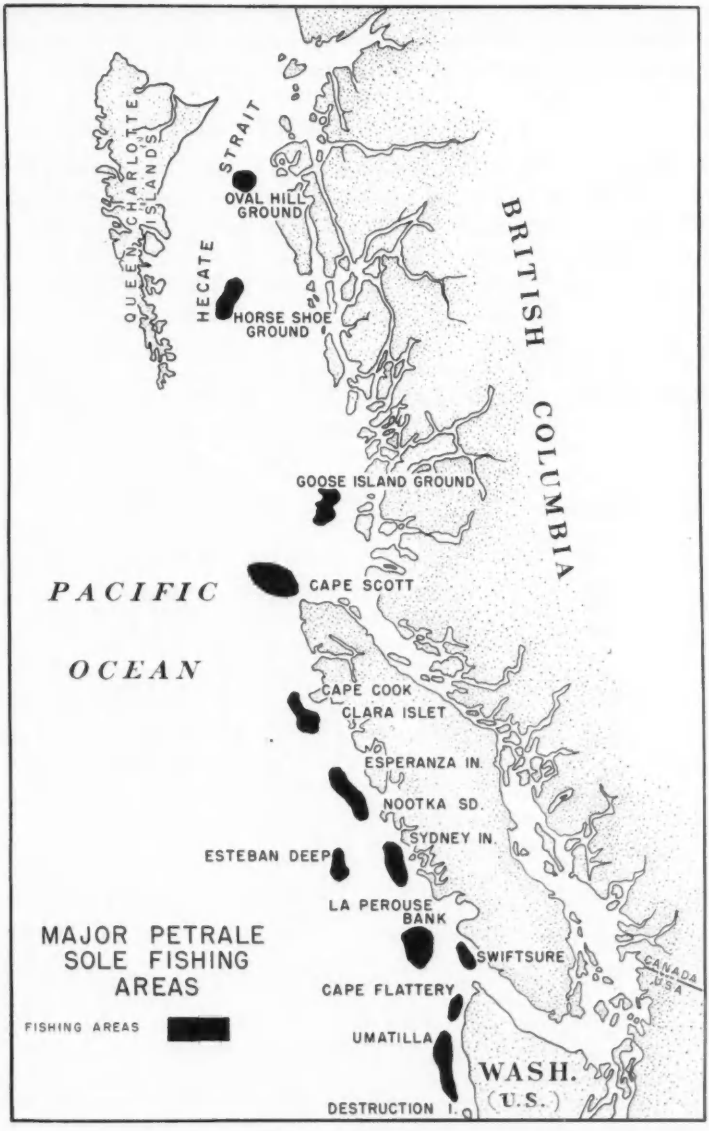

FIGURE 1. The general locations of some of the important petrale sole fishing grounds along the Washington and Vancouver Island coast.

to the discovery of deep-water stocks of petrale sole and their subsequent exploitation beginning in 1953 by the Washington trawl fleet. Since that time, the United States fleet has become increasingly dependent on this new fishery.

CATCH STATISTICS

The magnitude of United States landings of petrale sole, as related to total otter-trawl production for the period 1927 to 1937 is not known, as flatfish were not segregated by species in the statistics in those years. However, there is some information to suggest that by 1935, petrale sole stocks were being fished regularly by trawlers from Washington State: between 1935 and 1937 annual catches probably exceeded 1,000,000 pounds—as estimated from the trend of flatfish landings in subsequent years.

In Table I estimates are presented of total annual catch of petrale sole by British Columbia and Washington trawlers for the years 1938 to 1955 and in Tables IIa and IIb the catch by United States and Canadian vessels in major fishing areas.

TABLE I. Estimates of annual British Columbia and Washington landings of petrale sole, 1938–1955, in pounds.

Year	British Columbia	Washington	Total
1938	100,000	2,500,000	2,600,000
1939	125,000	2,300,000	2,425,000
1940	250,000	2,800,000	3,050,000
1941	250,000	4,400,000	4,650,000
1942	400,000	4,800,000	5,200,000
1943	450,000	6,000,000	6,450,000
1944	500,000	5,110,000	5,610,000
1945	810,000	5,553,600	6,363,000
1946	2,395,900	5,100,000	7,495,000
1947	1,762,340	4,800,000	6,562,340
1948	7,721,791	6,185,000	13,906,791
1949	3,291,939	4,870,000	8,161,939
1950	2,045,958	4,423,000	6,468,958
1951	1,585,306	3,400,000	4,985,306
1952	1,829,290	3,382,000	5,211,290
1953	1,049,191	2,445,000	3,494,191
1954	940,893	3,606,000	4,546,893
1955	582,325	2,900,000	3,482,325

TABLE IIa. Catch by area for United States vessels, 1948 to 1955, in pounds.

Year	Hecate Strait	Cape Scott and Goose Island	West coast of Vancouver Island		Washington coast	Esteban Deep
			Upper areas	Lower areas		
1948	1,143,509	1,317,478	1,890,956	1,501,853	227,979	
1949	2,013,243	558,358	479,762	1,469,192	279,383	
1950	1,178,365	951,576	1,184,200	785,220	253,384	
1951	869,550	482,647	487,960	1,090,826	424,109	
1952	1,078,632	493,557	389,777	918,200	480,351	
1953	466,413	853,086	243,878	500,295	67,520	250,000
1954	647,500	426,360	318,010	792,870	330,150	1,087,480
1955	141,420	966,784	235,689	466,139	406,071	683,957

TABLE IIb. Catch by area for Canadian vessels, 1945–1955, in pounds.

Year	Hecate Strait	Goose Island	Cape Scott	West coast of Vancouver Island[b] Upper areas	West coast of Vancouver Island[b] Lower areas	Queen Charlotte Strait	Strait of Georgia
1945	43,528	163,854	28,116	213,945	359,197	—	1,840
1946	426,024	684,406	67,906	404,168	805,506	5,275	2,615
1947	1,055,800	163,966	124,960	123,577	292,092	1,592	353
1948	5,475,709	575,174	111,761	156,455	1,402,219	378	95
1949	1,578,605	258,650	120,266	210,453	1,123,904	—	61
1950	347,377	155,995	129,671	324,874	1,086,911	—	1,130
1951	527,013	106,438	123,413	177,807	648,993	200[a]	1,442
1952	182,900	91,826	83,604	192,399	1,277,290	55	1,216
1953	66,520	64,607	41,588	29,357	843,153	1,471	2,495
1954	18,279	40,688	31,794	135,956	707,540	145	6,491
1955	26,260	8,468	16,485	199,863	330,099	300	850

[a]From Canadian Statistical Area 13 (lower Johnstone Strait–upper Strait of Georgia).
[b]West coast of Vancouver Island catches are divided geographically at Esteban Point, upper areas to the north and lower areas to the south.

These records have been derived from various sources. The Canadian catches prior to 1945 were based on the trend in total flatfish production and qualitative information on the growth of the west coast of Vancouver Island fishery for petrale sole. The 1945 and 1946 catches were based on log-book information and weighted to total flatfish production as computed by the Federal Department of Fisheries. From 1947 to the present an interview system conducted by port observers has provided coverage of the fishery.

The Washington records for the earlier years are likewise only approximations. The 1938–42 catches were estimated on the basis of the ratio of petrale sole landings to total flatfish landings in the period 1942–50. Records for 1943–47 were obtained from the Fishermen's Marketing Association of Washington, Inc., while those for the years 1948–53 were obtained from statistics of the Washington State Fisheries Department. In the more recent years a trip interview system, similar to that used in British Columbia, has been adopted (Alverson, 1955).

The growth of the petrale sole fishery is shown in Table I. Over two million pounds annually were landed by Washington trawlers in the early years, but the fishery was delayed in British Columbia at least in part as a result of a relatively greater interest by Canadian fishermen in fishing for dogfish. The total catch reached a peak in 1948, largely through the discovery of dense schools of fish on banks in northern Hecate Strait (Oval Hill and White Rocks grounds) and Canadian trawlers accounted for the greater part of the catch in that year.

Since 1948 the annual catches of petrale sole by trawlers of both nations have declined markedly. They fell more rapidly in the Canadian fishery, apparently because of the smaller size and shorter range of vessels comprising the Canadian fleet, and hence their lesser ability to offset declining yield on the more accessible grounds by expansion to more distant grounds and deeper water.

The decline in yield from inshore grounds along the west coast of Vancouver Island has been indicated by a decline in catch per unit of effort which is

associated in part with a decline in recruitment (Barraclough, 1954a). The decline in yield by the Washington fishery on these grounds has been offset in recent years (since 1953) by extension of fishing into deep water, particularly in an area known as the Esteban Deep (see Table IIa). The evolution of this fishery is described in the following section.

DISCOVERY OF DEEP-WATER FISHING GROUNDS

Prospecting of grounds along the continental slope adjacent to British Columbia, began in the early 1950's in response to increased demand for the deep-water rockfish (*Sebastodes alutus*) and to a lowered abundance of bottom fish on shallow grounds on the continental shelf (less than 100 fathoms). In the course of these explorations, Washington trawlers, in March 1953, discovered a dense stock of petrale sole about 27 miles south-southwest of Esteban Point on Vancouver Island and between depths of 170 and 250 fathoms. The productive ground when first discovered was relatively small, being about 6 miles long and half a mile wide. Henceforth this ground will be referred to as the Esteban Deep to distinguish it from other grounds adjacent to Esteban Point but in shallower water.

The topography of the Esteban Deep ground is similar to the general slope areas along the Washington and British Columbia coasts, the gradient being relatively steep and the bottom consisting of gray clay, strewn occasionally with large boulders. At the time of the discovery few trawlers were equipped to fish at depths over 110 fathoms and only six vessels were known to have engaged in the fishery. Interview records show that during late March and early April 1953, approximately 250,000 pounds of petrale sole were taken from the Esteban Deep.

In order to fish on this deep-water ground many fishermen had, by the winter of the following year, equipped their vessels with more cable in anticipation of a seasonal recurrence of petrale sole on this deep-water ground. The first catch from the Esteban Deep in 1954 was reported on January 20; however, no further landings were made until March 22 when the United States trawler *Aloma* delivered 70,000 pounds to Seattle. This catch, made in two days' fishing, was the largest single landing on record of petrale sole caught by a Washington trawler. On March 25 the trawler *Paragon* landed in Seattle approximately 90,000 of petrale sole. This catch was made in 2½ days' fishing on the Esteban Deep. The heavy concentration of petrale sole on this ground was evident in the fact that the catch per hour averaged in excess of 2,000 pounds during the first ten days of fishing. This was in marked contrast to the catch/effort on other grounds and at other seasons of the year, which was usually only a few hundred pounds. These landings resulted in a rush of boats to the area and within three weeks approximately 900,000 pounds were landed by a fleet of 20 United States trawlers. The Canadian fleet, not equipped for deep-water fishing and generally not active in the west coast of Vancouver Island winter fishery, did not fish the Esteban Deep. The total 1954 Esteban Deep catch, approximately one million pounds, represented about 30% of the petrale sole catch landed in the State of Washington for that year.

The discovery of the Esteban Deep aroused considerable interest, not only because of the dense concentrations of petrale sole, but also because the depth where they were found was far greater than had previously been reported in commercial operations off the British Columbia and Washington coasts. To the fishermen it was a new source to augment dwindling catches from the shallower inshore grounds. Its contribution to landings in future years will be affected by regulations promulgated in January 1956, which prohibit the landing of petrale sole in the States of Washington and Oregon during the period February 1 to April 15, except that incidental catches not to exceed 6,000 pounds per trip can be marketed.

SAMPLING AND PRELIMINARY OBSERVATIONS

The sudden discovery and short duration of the deep-water fishery in 1953 precluded other than cursory observations being made at that time. Whether or not the presence of the stock in the Esteban area was of regular annual occurrence could be determined only by future observations. In anticipation that there would be a recurrence of this fishery, a more elaborate preparation was made for investigating the fishery in the following season. Petrale sole appeared on the Esteban Deep grounds in January 1954, but dense concentrations were not reported until March.

Between January and April 1954 the fishery was closely watched and market samples of petrale sole were taken at the ports of Bellingham and Seattle, and data were recorded as to the size distribution, sex ratio, and degree of maturity. A noteworthy feature was the predominance of females occurring in the samples taken early in the fishery and their decrease as the season progressed (Table III). At first it was thought that this shift in the sex ratio was the result of a change in the pattern of fishing. However, interviews with a number of the vessel captains revealed that this factor could be discounted. Sampling the succeeding years of 1955 and 1956 confirmed the predominance of female fish in the early catches. This changing sex ratio during the spawning period is apparently an inherent reproductive pattern characteristic of the Esteban Deep stock.

Studies were made on the filleted carcasses of petrale sole, and by careful examination of the ovaries of specimens the state of maturity was recorded in terms of the following classifications:

(1) *running ripe*–ova mature, clear and free flowing.
(2) *ripe*–ovaries distended and ova extrusible with moderate external pressure.
(3) *developing*–ovaries well developed but discharge of ova not possible by moderate external pressure.
(4) *immature*–ovaries slightly developed or not at all.
(5) *spent*–ovarian tissue shrunken and flaccid, no ova discharged by heavy external pressure.

The results of this study are presented in Table III.

TABLE III. Condition of petrale sole ovaries in relation to time and the percentage of males in samples taken in 1954 from the Esteban Deep. (See the text for the the scale of "conditions".)

Date	Condition of female fish					Percentage males
	1	2	3	4	5	
January 20	1.9	93.3	0.6	0.6	3.7	17.9
March 23	17.6	67.5	0.0	0.0	14.8	—
March 30	34.0	52.0	0.0	0.0	14.0	59.0
April 1	31.8	36.1	0.0	0.4	31.6	62.6
April 7	35.5	55.5	2.7	0.0	6.4	64.3
April 16	24.4	2.2	0.0	2.2	71.1	85.9

All of these classifications, with the exception of number (4), represented fish which would have or had spawned during the season of observation. Of 1,172 females examined, less than one-half of one per cent were recorded as being immature.

Sampling studies revealed a population composed almost exclusively of fish accumulated for spawning. Measures of the length-frequency distribution of fish captured on the Esteban Deep grounds did not reveal small immature individuals, which at times occur along with adult fish taken by the inshore fisheries later in the year (Fig. 2a). Females sampled from Esteban Deep catches during 1954 ranged from 35 to 60 cm. in length (from the end of the head with mouth closed to the tip of the median rays of the tail), with a mean length of 47.81 cm. and the lengths of the males ranged from 33 to 48 cm. with a mean length of 40.96 cm.

Decreasing percentage representation of females evident in the market samples as the season progressed probably resulted from an emigration of that sex as soon as spawning was completed, and a measure of the percentage of the total female population spawned in relation to time was not possible. Unfortunately, lack of detailed information on the short-term trend in catch/effort also prevented quantitative study of the change in sex ratio. The observations do indicate spawning commencing as early as January. However, maturity studies indicate peak spawning probably is reached in the latter part of March and probably terminates in April. Shortly thereafter the fish move off the grounds and are absent until the following winter.

RECOVERIES FROM INSHORE CANADIAN TAGGINGS

There were three possibilities as to the relation of spawning stock in the Esteban Deep to those which for many years had been exploited on inshore grounds: (1) that it was independent of the inshore stocks, and had heretofore remained unexposed to fishing prior to its discovery, (2) that it was drawn from closely adjacent inshore grounds, or (3) drawn from inshore grounds along a wide range of the coast. Tag recaptures discussed below from Canadian experiments conducted on inshore grounds prior to the discovery of the Esteban stock, supported the third possibility.

At various times between 1945 and 1954, the Fisheries Research Board tagged and released petrale sole on many of the major inshore trawling grounds adjacent

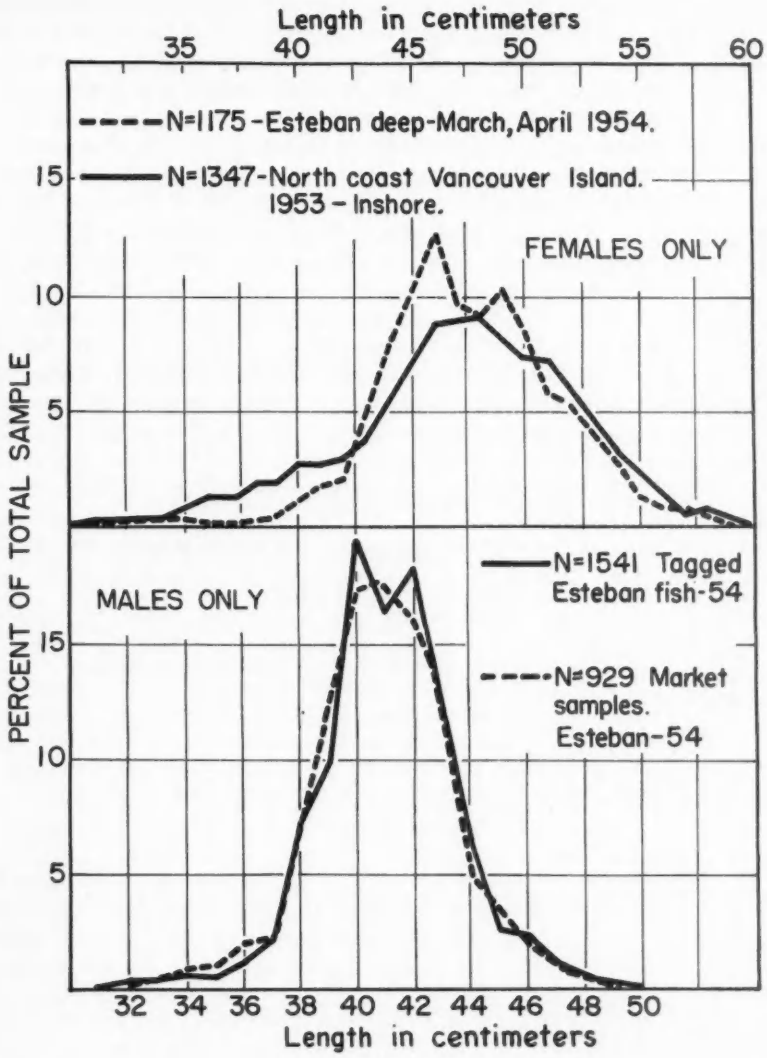

FIG. 2a. Length frequencies for Esteban Deep female petrale sole and those for the north coast of Vancouver Island (inshore) 1954.

FIG. 2b. Length frequency distributions for male tagged petrale sole and male market sampled petrale sole caught at Esteban.

to the British Columbia coast. Recaptures from these taggings are summarized in Table IV. In general, the results from these taggings did not reveal any regular migratory pattern for this species, but rather erratic movements in a northerly or southerly direction from the areas of tag release. For most of this period trawling was confined to the shallower inshore grounds.

The development of a deep-water fishery led to the recovery of a number of these tags on the Esteban spawning ground. Barraclough (1954b) reported a total of 15 Canadian-tagged fish recaptured during the winter fishery off Esteban in the years 1952–54 inclusive. Of this total, 13 had been tagged and released on trawling grounds in Hecate Strait and Queen Charlotte Sound, and only 2 were from closely adjacent inshore grounds off the west coast of Vancouver Island. In February and March 1955, 3 additional Canadian-tagged petrale sole were recovered by the Esteban fishery. Two were from releases on the Goose Island grounds in Queen Charlotte Sound during May 1952 and 1954, and one was from a tagging conducted nearby at Sydney Inlet, on the west coast of Vancouver Island in 1951.

TABLE IV. Number of Canadian-tagged petrale sole released off the British Columbia coast and total recoveries by Canadian and United States trawlers to May 30, 1956.

	Area of release			
	Hecate Strait	Queen Charlotte Sound	West Coast Vancouver Island	Total
Number tagged	1,141	1,054	3,605	5,800
Tagging period covered	1945–54	1949–54	1945–51	...
Numbers recovered off Canada				
By Canadian vessels	113	52	706	871
By U.S. vessels	52	176	232	460
Numbers recovered off Washington				
By U. S. vessels	2	5	41	48
Grand total	167	233	979	1,379

From all petrale sole taggings conducted by Canada on inshore stocks a total of 18 Esteban recoveries have been made, of which 15 had been tagged and released in the waters of Hecate Strait and Queen Charlotte Sound, several hundred miles to the north of the Esteban spawning ground. The fact that only three of the tags recaptured at Esteban were from taggings conducted on inshore grounds off the southwest coast of Vancouver Island was surprising, in that a far greater number of Canadian tags have been released on inshore grounds off the west coast of Vancouver Island than on grounds farther to the north (see Table IV). This suggested that the northern areas contributed substantially more to the Esteban spawning stocks than did areas off the west coast of Vancouver Island.

Other returns from tagging conducted on these southern inshore grounds suggest a movement to spawning grounds off the Washington and Oregon coast in winter time (Chatwin, MS). Little mingling can be demonstrated between

inshore stocks on the grounds off the lower west coast of Vancouver Island and those farther to the north. Only 9% of the 979 fish captured showed a movement to the north; 67% were recaptured in the general area of release, and 21% showed a movement to the south. Recovery information on the remaining 3% was not obtainable.

TAGGING ON THE ESTEBAN SPAWNING GROUND

Early in 1954, tagging was conducted on the newly discovered Esteban spawning ground to determine the dispersal pattern of spent fish from this area and thus confirm or disprove the preliminary evidence derived from earlier Canadian experiments. Although Canadian fishing vessels have not participated in the Esteban fishery to date, it seemed desirable that both United States and Canadian research agencies should be involved because of the international nature of the fishery on the major inshore banks along the British Columbia coast. Accordingly, Canadian and United States scientists carried out a tagging experiment aboard the chartered United States trawler *Heather* between April 9 and 11, 1954, on the spawning ground 25 to 30 miles south-southwest from Esteban Point, Vancouver Island. The experiment was repeated on March 23 to 28, 1955, with the United States Fish and Wildlife Service vessel *John N. Cobb*. The results of these two tagging operations are reviewed in the following sections.

Esteban Deep Tagging Experiment—1954

The period originally assigned for this tagging was from April 5 to 13, 1954. However, because of adverse weather conditions, there were only three days of effective tagging. The type of tag used was the Petersen disc, attached to the fish by means of a stainless steel pin on the mid-point of the body near the base of the dorsal fin. Ten drags which varied in duration from 1 to 2½ hours were made with a 350-mesh commercial trawl net constructed of 4½-inch mesh (stretched measure, between knots). After the catch in each haul was brought on board and released on deck, the petrale sole were immediately separated from other species and placed in a canvas live-tank. As might be expected of fish brought up from a depth of 200 fathoms, their physical condition was poor. Their condition was further aggravated by the continual heaving motion of the water in the retaining tank, and as a result very few fish were in suitable shape for tagging. On liberation, the behaviour of each tagged fish was noted. About one-half of the total releases descended immediately while the other half remained on the surface for varying periods of time. In several instances, black-footed albatross were seen to attack, and undoubtedly kill, some of the surface-swimming tagged fish. Under these various adversities it was concluded that mortality of tagged fish would be great; the exact extent, of course, was indeterminable.

A total of 1,795 fish was liberated, of which 922 were identified with Canadian tags and 873 with United States tags. Of this total, 1,544 were males, 248 were females, and 3 were unidentified as to the sex. The unbalanced sex ratio of the

tag sample, 6 males to 1 female, as shown earlier, was a reflection of the sex ratio characteristic of the stock fished at that stage in the spawning season.

Because only those fish which appeared to be in good condition were selected for tagging, it might be expected that the size and sex composition of these fish differed from that of the stock present on the grounds at the time of tagging. However, a graphic comparison of the frequency distributions of tagged fish for 1954 with those of market samples taken from the commercial landings demonstrates that the distributions were similar (Fig. 2). According to Harry (1956), petrale sole greater than 32 cm. in length are physically available to trawl mesh of 4½ inches stretched measure between the knots.

Recovery of Tagged Fish

A total of 41 or 2.2% of the total tagged petrale sole (24 Canadian and 17 United States tags) was recovered to May 30, 1956, from fish released off Esteban in 1954. These results are summarized in Table V by years and show the recoveries by Canadian and United States vessels. The dispersal of the 41 tagged petrale sole recaptured by the commercial fishery is illustrated in Figure 3a.

Table V. Recoveries from 922 Canadian and 873 United States tags released in 1954 at the Esteban Deep, to May 30, 1956, by Canadian and United States trawlers, arranged by year of recapture and nationality of the vessels making the recapture.

Kind of tag	Canadian		United States		Both kinds		
Vessels making the recaptures	Canada	U.S.	Canada	U.S.	Canada	U.S.	Both
1954	3	5	–	6	3	11	14
1955	2	8	1	7	3	15	18
1956	–	6	–	3	–	9	9
Total	5	19	1	16	6	35	41

The arrows in Figure 3a show the net movement and possible migration routes of the recaptured fish from the Esteban Deep. It is recognized that erroneous conclusions on the migrations of fish stocks might be drawn from tagged fish recaptured by the commercial fishery, in view of the fact that the rate of exploitation varies from area to area. Consideration of this effect is discussed in a later section.

On the basis of the proportion of the total recaptures to May 30, 1956, taken in major fishing areas, the north coast areas (Cape Scott to Hecate Strait) accounted for 9 or 21.9% of the total. The northwest coast of Vancouver Island areas yielded 10 or 24.3% of the total returns, and the Esteban Deep 15 or 36.5%. Only 4 or 9.7% of the tagged petrale sole recaptured had indicated movement directly inshore or southward from the tagging area. Three returns, or 7.3%, were unassignable to an area of capture.

During April 1954 (within a month after tagging), 4 tagged fish were recaptured in or near the tagging area. Two were taken from the Esteban Deep in 165–210 fathoms, and 2 were taken from grounds southeast of Esteban

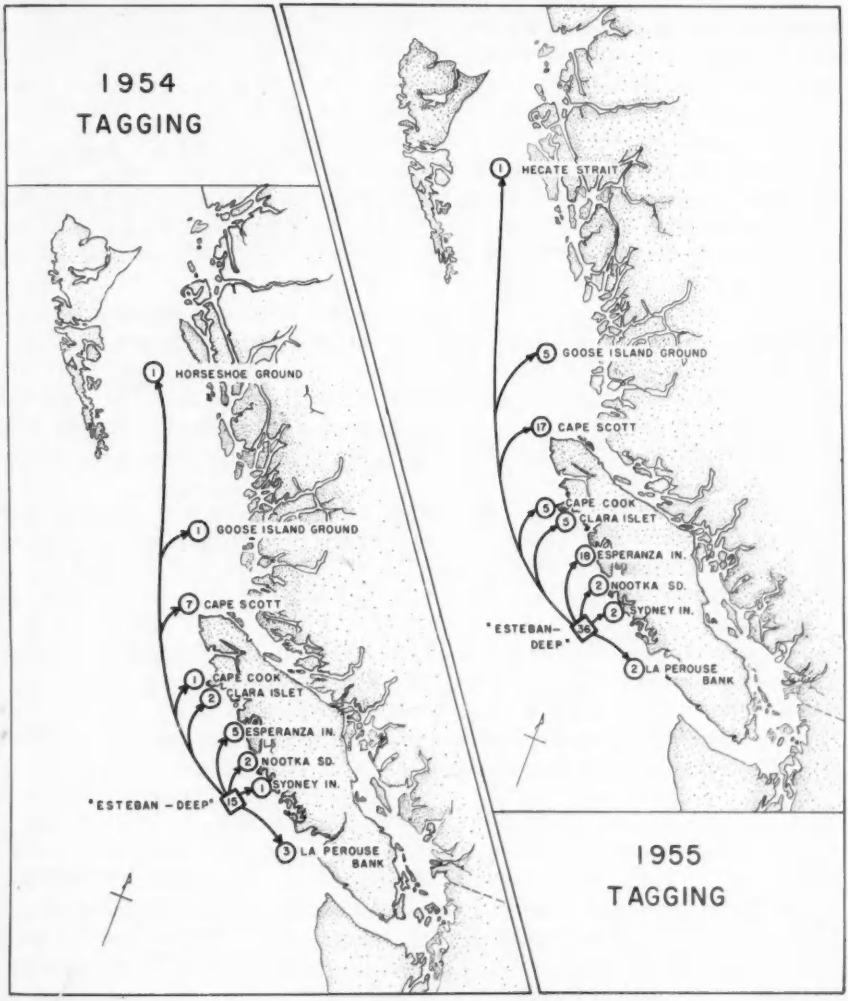

FIG. 3a. Distribution of tagged petrale sole recovered to May 30, 1956, from fish tagged and released on the Esteban Deep, April 9–11, 1954.

FIG. 3b. Distribution of tagged petrale sole recovered to May 30, 1956, from fish tagged and released on the Esteban Deep, March 23, 24, 27 and 28, 1955.

Point in 45 fathoms. Four other returns during this same month indicated northerly movements into shallower water. One was from Nootka Sound in 42 fathoms, and 3 were from Esperanza Inlet in 67–70 fathoms. In the succeeding spring and summer months, 4 recaptures were made–1 from a ground 14 miles southwest of Sydney Inlet in 48 fathoms during May, 1 off Nootka Sound in 30 fathoms during July, 1 from La Perouse Bank in 41 fathoms and 1 from the Horseshoe grounds in northern Hecate Strait in 50–55 fathoms during August. In the fall and winter months of 1954–55, 4 recaptures were reported; 1 from the La Perouse or Big Bank in September, 2 from the Cape Scott bank in January and February. Another one was reported caught in the Cape Scott area but no exact date of recapture was given.

The seasonal occurrence of tag returns in 1955 indicate a similar pattern to that shown by the tagged fish recaptured in 1954. During the period of the spawning season in March 1955, 6 recaptures were made in the Esteban Deep. From March to August 1955, 7 recaptures were made during the inshore fishery from Esperanza Inlet northward to Cape Scott. In the months of November and December 1955, 3 tagged fish were reported–2 from Cape Scott and 1 from La Perouse Bank.

During March and April 1956, the second spawning season following the time of tagging, 9 more recaptures were made. Five tagged fish were from the Esteban Deep, 1 was from Cape Cook in 75 fathoms, 1 was from Queen Charlotte Sound in 55 fathoms, and 2 were undesignated as to time or area of recapture.

In spite of the low recovery rate (2.2% to May 30, 1956), migration pattern favouring a northerly dispersion was indicated to shallower inshore areas during the summer months, with a subsequent return to the spawning ground on the Esteban Deep in the late winter. These results supported the conclusions drawn from the earlier Canadian experiments.

Esteban Deep Tagging Experiment–1955

The Esteban Deep tagging experiment was repeated in 1955 and carried out aboard the United States Fish and Wildlife Service Vessel *John N. Cobb* on March 23, 24, 27 and 28, with similar gear, tags and methods of tagging. However, unlike the 1954 experiment, the time taken for each of the 16 drags was shorter, varying from ½ to 1 hour. Weather conditions during the days when tagging was carried out were more favourable than those encountered in 1954. These factors, in addition to the use of a larger more stable vessel, resulted in a general improvement in the condition of the petrale sole which were tagged. This was most apparent when it was observed that the majority of the fish released descended from the surface almost immediately on contact with the water.

As a result of the more favourable conditions prevailing at the time of tagging, the number of tagged petrale released was greater than in 1954. During this experiment, 2,007 tags were applied, of which 1,194 were Canadian and 813 were State of Washington. Although the tagging in 1955 occurred two weeks earlier than that of 1954, a preponderance of male fish in the tagged sample was

again evident (11 males to 1 female). Thus the results, like those from the previous year's tagging, apply principally to male fish. However, there is nothing in existing information on sex segregation on the inshore grounds to suggest that dispersal of male fish is radically different from that of the females.

Because of the improved conditions in 1955, discard of damaged fish was negligible, and, for the most part, the entire catch of petrale sole in each tow was tagged. As standard commercial trawling gear was used, the tagged fish were considered to be representative of those available to the trawl fleet.

A comparison of different sizes of fish tagged is as follows (males only):

Size	*Tagged*	*Recaptured*	*Percentage recaptured*
Less than 41 cm.	730	30	4.11
41 cm. and larger	1,103	61	5.53

Although the returns suggest that soles smaller than the modal size of 41 cm. were less able to withstand the effects of tagging than fish of greater size (the latter were returned 35% more often), the χ^2 computed on the basis of the expected and observed returns is only 1.52 (with Yate's correction) so that no real difference can be proved from this small number of returns.

The recoveries of the two sexes were as follows:

	Tagged	*Recaptured*	*Percentage*
Male	1,833	91	4.97
Female	174	12	6.89

The recapture of females was 39% greater than that of males, but there is even less assurance that this is not just accidental ($\chi^2 = 0.70$). Because the size and sex differences between tagged and recaptured fish are small and are not proven to be real, the data have been treated as a whole in the developments which follow.

Recovery of Tagged Fish

Table VI summarizes the recaptures by Canadian and United States vessels following the 1955 tagging. A total of 103 tags (59 Canadian and 44 United States) or 5.1% of the total number tagged were returned to May 30, 1956, by the commercial fishery. The increase in the success of recovery of tagged fish

Table VI. Recoveries from 1194 Canadian and 813 United States tags released in 1955 at the Esteban Deep, to May 30, 1956, by Canadian and American trawlers, arranged by year of recovery and nationality of the vessels making the recapture.

Kind of tag	Canadian		United States		Both kinds		
Nationality of vessel	Canada	U.S.	Canada	U.S.	Canada	U.S.	Both
1955	19	18	7	24	26	42	68
1956	1	21	1	12	2	33	35
Total	20	39	8	36	28	75	103

from the 1955 experiment over that of the 1954 experiment (total returns of 5.1% and 2.2% respectively) is more likely the result of the better condition of fish tagged in the more recent experiment, than of a greater rate of exploitation. However, there is no way to separate these two factors.

The distribution of the 103 tagged fish recaptured from the 1955 tagging on the Esteban spawning ground is illustrated in Figure 3b. A comparison of Figures 3a and 3b shows that the general dispersal patterns resulting from the two experiments are similar. The percentage of total recoveries of tagged fish recaptured in each of the four major fishing areas was also very similar. The north coast areas (Cape Scott to Hecate Strait) accounted for 24, or 23.3% of the total, while the northwest coast of Vancouver Island accounted for 30 or 29.1%, and the Esteban Deep 36 or 34.9%. Recoveries which showed a movement directly shoreward or southward from the Esteban Deep, were 4 or 3.8%—less than that recorded from the 1954 experiment. Nine or 8.7% lacked information on area of capture.

The 103 tagged fish here reported from the experiment conducted in 1955 were accounted for during a period little more than one annual cycle from the time of tagging; i.e. from the 1955 spawning season through the next, and into the late spring of 1956. The distribution of returns during this one season is not unlike the result from the earlier experiment in 1954, and the returns are greater in number.

Immediately following tagging in March and April 1955, a total of 18 tagged petrale were recaptured—11 were caught at the Esteban Deep, 6 were returned from inshore areas off the northwest coast of Vancouver Island (2 from off Esperanza Inlet in 62 fathoms, 4 from Clara Islet near Cape Cook in 30–42 fathoms), and 1 was taken a month after tagging from the southeast edge of the Goose Island ground in Queen Charlotte Sound.

During the late spring and summer months, May to August inclusive, 32 recoveries were reported. With the exception of 4 tags, 2 of which were unreported as to area and date of recapture and 2 of which were taken either from nearby Sydney Inlet or at Longbeach, Vancouver Island, all were captured in areas to the north of the tagging area. Eighteen were captured along the northwest coast of Vancouver Island in the area from Nootka Sound to Cape Cook, 5 were taken on the Cape Scott bank, 4 were caught on the Goose Island ground in Queen Charlotte Sound, and 1 was caught in Hecate Strait near Bonilla Island.

In the fall of 1955 and the winter of 1955–56, during a period from September to January inclusive, a total of 16 tagged fish were returned—10 recaptures were made on the Cape Scott bank, 3 in the Esteban Deep, 2 on the La Perouse or Big Bank (indicating a southerly movement), and 1 for which no information was given.

From February to May 1956, 22 tagged petrale were recaptured in the Esteban Deep, 5 were caught in inshore areas off the west coast of Vancouver Island and to the north of the tagging area, 1 was caught on the Cape Scott bank, and the origin of 4 was either uncertain or not stated. The dates of recapture for

5 tagged fish were not reported. Of these, 1 was taken from Hecate Strait, 2 from the Cape Scott grounds, 1 from Cape Cook, and 1 was of unknown origin.

Recoverability of Canadian and United States Tags

As mentioned previously, two groups of tags were liberated during each experiment; one lot with instructions requesting return of the discs to the Fisheries Research Board of Canada and the other to the Washington State Department of Fisheries. The division into two groups allowed a comparison of the recoverability of the tags. In 1954 and 1955 the ratio of Canadian to United States tags released was 51.3 to 48.7% and 59.4 to 40.6%, respectively. Assuming the tagging mortality was approximately equal for both groups, the recovery ratio would be expected to be similar to that at the time of release. This also presumes that fishermen of one country are just as conscientious about returning tags belonging to the other country as they are their own. The recovery ratios computed to May 30, 1956, were 58.5 to 41.5% for 1954 and 57.2 to 42.7% for 1955. Chi-square tests showed no significant difference between the expected returns and those observed.

Recoveries in Relation to Distribution of Fishing Effort

The possibility that the observed patterns of dispersal of tagged fish are biased by the pattern of fishing effort is discounted after consideration of Table VII. Had fishing effort been much greater to the north of Esteban Point, then the observed pattern of tag recovery could have resulted even if the tagged fish dispersed in equal numbers to the north and south of that point. As shown in Table VII, the distribution of effort was actually slightly greater to the south.

Following the 1954 tagging experiment, 54.7% of the total inshore effort (Canadian and United States) was expended south of Esteban Point and 44.6% of the total petrale sole catch was made south of the Point. Following the 1955

Table VII. Total catch of petrale sole and total effort subsequent to the 1954 and 1955 tagging experiments, according to major fishing areas (Canadian and United States catch and effort combined).

	Esteban Point south to Destruction Island	Esteban Deep[a]	Esteban Point north to Cape Scott	Cape Scott to Hecate Strait
1954 tagging, May 1, 1954 to May 30, 1956				
Total catch (*lb.*)	2,874,129	1,083,600	939,177	2,626,185
Total effort (*hr.*)	48,749	3,065	7,031	33,272
1955 tagging, April 1, 1955 to May 30, 1956				
Total catch (*lb.*)	1,099,381	481,430	518,091	1,228,565
Total effort (*hr.*)	26,269	2,028	5,250	20,011

[a]Esteban Deep fishery January through April inclusive.

experiment, 51.0% of the total hours fished was recorded for the area between Esteban Point and Destruction Island while 38.9% of the total catch was made in that area. The small number of recoveries south of Esteban Point, 3 in 1954 and 2 in 1955 with equal or better opportunity of recovery in that area, precludes the possibility that the observed northward dispersal from the Esteban spawning ground is a reflection of a greater fishing intensity to the north of Esteban Point than to the south.

DISCUSSION OF RESULTS

Movements of Petrale Sole

The seasonal distribution of recoveries during 1955 and 1956 indicates that the Esteban Deep stock disperses after spawning and that during the late spring and early summer (April–June) its maximum density center occurs along the northwest coast of Vancouver Island; later it is in the Cape Scott–Queen Charlotte Sound area (Goose Island grounds) and Hecate Strait. The rate and pattern of northward dispersion may vary from year to year.

The evidence of highly migratory petrale sole manifest by these tagging experiments and by those reported by Barraclough (1954b) are in contrast to earlier results of Cleaver (1949) and of Harry (1956). Cleaver in his study of the petrale sole in the Cape Flattery area covering the period 1938–45 could show no well-defined pattern of migration, although its existence was not precluded. In the presence of a fishery which at that time was operating over only the shallower part of the petrale sole's annual vertical range, there was a tendency for tagged fish to show little movement. Cleaver recognized a marked annual periodicity in recovery time which he related partially to variation in fishing effort and reduced availability of the species during winter months. He also demonstrated a marked decrease in large fish available to the fleet at that time of year. In the light of more recent studies, Cleaver's observations may be attributed to a migration of mature fish to deep water in the winter months. Harry (1956) was unable to establish any seasonal movement for petrale sole inhabiting banks off the Oregon coast but he suggested the possibility of a shift to deep water. His conclusions were based on recoveries made prior to the inception of the deep-water fishery, and on a fishery which was much restricted in its winter activity. The movement of petrale sole to deep water (150 to 300 fathoms) at the time of spawning, while not yet substantiated by tagging results off the coast of the United States, is suggested by the recent discovery of several small spawning grounds off the Washington coast (off Cape Flattery, Destruction Island and Grays Harbor). Fishermen also report similar occurrences of petrale sole in certain deeps off the California coast.

This seasonal movement to deep water, in association with the spawning process, is a phenomenon which apparently is common to a number of flatfish in the northeast Pacific Ocean. It has been demonstrated for the Dover sole, *Microstomus pacificus*, through studies of seasonal catches by depth (Hagerman, 1952; and Harry, 1956), and for the lemon or English sole, *Parophrys vetulus*,

(Ketchen, 1956). However, the migrations of Dover sole and lemon sole do not appear to cover as wide an area as do those of the petrale sole.

The long migrations of petrale sole from summer feeding grounds and the "choice" of a specific deep-water spawning area arouse considerable interest as to the directive and causative factors involved in this process. Movements of as much as 350 miles have been recorded—from northern Hecate Strait to the Esteban spawning ground. The failure of fish tagged on the Esteban spawning ground to appear on other spawning grounds farther to the south in later years, and also the failure of fish tagged on the summer grounds adjacent to Vancouver Island to participate in the Esteban spawning in significant numbers, supports the view that the Esteban area is of specific attraction to stocks inhabiting waters of the northern British Columbia coast. The return of tagged fish for two successive years to a spawning ground (area of release) at the southern extremity of the indicated migration pattern suggests a homing tendency of this species to specific "deeps". It is not proposed that the progeny of Esteban fish or those from other deeps return exclusively to the parent area, but rather that after recruitment to a particular stock a fish will adopt the characteristic migration and spawning pattern of the group. The most cogent interpretation of the data available to date is that with the adults there may be homing tendency which is dependent on the adopted stock.

It is possible that, with the onset of maturity in the fall months, there is a response to the physical and chemical gradients which exist along the coast, and that the petrale sole is guided by these in its southward movement from Hecate Strait and Queen Charlotte Sound to deep waters off the west coast of Vancouver Island. However, in the absence of comprehensive knowledge of the dynamics of deep-water hydrographic conditions, or of an understanding of the complex responses of the petrale to such conditions, it is impossible to explore this possibility with confidence. The explanation of the apparent precision of the migration, and the selection of specific areas for spawning, therefore, remains a mystery for the time being.

Thompson and Van Cleve (1936), by means of drift bottles, demonstrated a net drift of surface currents northward and inshore along the British Columbia coast during the spring and summer months of the year. The pelagic young, like those of the halibut which spawn near Cape St. James, are presumably carried from the Esteban spawning ground northward along the coast, and are dispersed on banks lying along the west coast of Vancouver Island, in Queen Charlotte Sound and Hecate Strait. The theory of "upstream migration" to spawning grounds is supported at least by evidence of surface drift.

Contribution of the Esteban Spawning Stock to the Inshore Fishery

Washington landings of petrale sole from the Esteban Deep in 1954 and 1955 constituted 30% and 25%, respectively, of the total petrale sole landings in that State, and 24% and 21% respectively of the combined British Columbia and Washington landings. It is evident, therefore, that the fishery on the spawning stock has played an important role in the total production of recent years. A

qualitative appraisal of the inshore distribution of Esteban fish may be obtained through study of Figure 3b. The percentage of total inshore recoveries by area shows that the Esteban spawning stock contributed most to the inshore fishery between Esteban Point and Cape Cook. This assumes that tagged fish, when liberated, became randomly distributed among untagged fish *still on the ground* and that they remained so throughout the rest of the year. The Esteban stock also contributed a high percentage of fish to the Cape Scott–Hecate Strait fishery, but little to the area south of Esteban Point. Quantitative contributions may be estimated by calculating the total number of males in the landings for the major geographic subdivisions and thence the ratios of tagged to untagged for these regions (Table VIII). The total males in numbers (T_m) (line 6, Table VIII) in the catch from each area was calculated as:

$$T_m = \frac{C}{P_m \cdot \overline{w}_m + P_f \cdot \overline{w}_f} \times P_m,$$

where C=the total catch for the area in pounds,

P_m=the percentage of males in samples, in numbers.

$\overline{w}_m$=the mean weight of males for that area,

P_f=the percentage of females in samples, in numbers, and

$\overline{w}_f$=the mean weight of females for that area.

TABLE VIII. Combined United States and Candian petrale sole catch by area and calculated contribution of Esteban stocks to the inshore fisheries (April 1, 1955–May 31, 1956).

	Esteban Point south	Esteban to Cape Cook	Cape Scott to Hecate Strait	Esteban Deep (1956 only)
(1) Catch (*lb.*)	1,099,381	518,091	1,228,565	348,000
(2) Tag recoveries	4	30	24	25
(3) Percentage of inshore recoveries	6.9	51.7	41.4	–
(4) Male tag recoveries	4	24	18	25(20)[a]
(5) Percentage males in market samples	28.7	38.8	44.6	72.4
(6) Calculated males in landings	109,884	71,860	169,818	62,799
(7) Tagged to untagged ratio	1:27471	1:2994	1:9434	1:3140
(8) Calculated percentage inshore males from Esteban Deep	11	100	32–33	–

[a]Number of returns after March 10 used to calculate Esteban tag ratio.

The percentage by numbers and mean weight for each sex has been estimated from market samples of landings from the various areas. In calculating the ratio of tagged to untagged petrale sole for the Esteban area, only the recoveries and the catch made after March 10, 1956, were used. This was necessary as sampling was not adequate to determine the sex ratio existing prior to that time. A tagged to untagged ratio could not be estimated for the Esteban Deep area in 1955 as only minor fishing occurred on the grounds after tagging. The ratio of tagged to untagged male fish in each of the major fishing areas is shown in line 7, Table VIII (line 6 divided by line 4). In one of the three inshore divisions of the coast–Esteban to Cape Cook–the ratio of tagged to untagged is very similar to that for

Esteban Deep. In the Cape Scott to Hecate Strait region, however, this ratio is only one-third as great, and south of Esteban Point it is only one-ninth as great. This suggests a mingling of Esteban fish, in the northern region, with stocks which did not participate in the Esteban spawning or which had participated earlier. Mixing with other stocks is also suggested in the area south of Esteban.

Assuming random movement of the tagged males after release in a tagged: untagged ratio similar to that observed for the Esteban stock (1:3140), and that this ratio remains constant in all areas at any instant of fishing following tagging, then the numbers of recoveries expected in each of the major areas of recovery may be calculated directly by proportion. The actual recaptures, in line 4 of Table VIII, expressed as a percentage of the theoretical number expected, indicates the percentage contribution of Esteban male fish to the inshore fisheries. These estimates are shown in line 8, Table VIII. Sampling error, tag loss, recruitment and a differential mortality rate between tagged and untagged fish in the period for which tag ratios were computed would, of course, materially affect these estimates. Also, it is noted that the calculations are based on only the late season and dominantly male segment of the spawning stock. However, the model illustrates that the Esteban male stock contributes substantially to the inshore fishing areas north of Esteban Point, in this case approximately 53% of the total catch.

The number of female petrale sole tagged and the number recovered is not sufficient to compute estimates of the Esteban female contribution to the inshore fisheries. Only 12 tagged females were recovered from the inshore catches—6 in the Esteban Point to Cape Cook area and 6 in the Cape Scott to Hecate Strait area. It is suggested therefore that the Esteban females may also contribute greatly to the total catch in the northern areas.

Effect of Stock Movements on the Fishery

Marked variations in the catch per unit effort as a measure of annual availability of petrale sole on particular grounds is indicated from past observations of the fishery. These short-term changes in yield are possibly a reflection of the highly mobile characteristics of the petrale sole stocks, rather than a direct result of an absolute change in stock or population size. In the fishery for petrale sole, as much as 70 to 80% of the total annual catch from a particular ground may be taken during a period of 4 to 8 weeks, after which the fish are absent from the grounds. Seasonal movements of the petrale sole along the coast in association with the spawning process, i.e. north to south for spawning, are in many ways analogous to the movements shown for the halibut in the Gulf of Alaska (Thompson and Herrington, 1930). Annual variations in the movements of halibut stock through these regions could conceivably result in a year-to-year variation in the numbers of adults available to capture on these grounds. Undoubtedly the effects of fishing and other causes are major factors influencing trends in stock size; however, it is possible that short-term fluctuation in the catch per unit of effort of flatfish stocks may be materially affected by the occurrence of seasonal variations in migrations of a species.

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Variation in the Incidence of Larval Nematodes in Atlantic Cod Fillets along the Southern Canadian Mainland[1]

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ABSTRACT

The incidence of larval nematodes, *Porrocaecum decipiens*, in fillets from three size-groups (scrod, market and steak) of Atlantic cod, *Gadus callarias*, has been analyzed. The analysis was based on about 73,000 fillets from cod caught between 1946 and 1956 in about 20 areas off the southern Canadian mainland.

Geographic variation in the percentage of fillets infected was found in all size-groups of cod. For market cod the incidence ranged from a low of 6% on the offshore Nova Scotian Banks to a high of 35 to 91% in the southwestern Gulf of St. Lawrence. Intermediate values of 14% and 22% were observed respectively in the inshore fisheries of western Nova Scotia and Cape Breton Island. Similar patterns of geographic variation were present in scrod and steak cod. The main geographic differences in incidence were related to the distribution of the harbour seal (*Phoca vitulina*), the harp seal (*Phoca groenlandica*) and the gray seal (*Halichoerus grypus*).

Incidences of infection and the number of nematodes per fillet usually varied directly with the size of the cod. The number of nematodes per pound of fillet was usually inversely related to the size of cod. It was concluded that cod could become infected throughout life and that the highest rate of infection occurred in small cod.

Local variations, as distinct from broad geographic variations, were observed in the areas of Lockeport, of Cape Breton Island and of the southwestern Gulf of St. Lawrence. In these areas, the cod caught closest to shore were usually the most heavily infected.

Seasonal variations in incidence occurred in the Cape Breton and Lockeport fisheries. The highest incidences occurred in the spring and fall in Cape Breton cod and in the summer in Lockeport cod. The variation in the Cape Breton fishery was attributed to seasonal migrations of the cod comprising the fishery. Increased use by fishermen of shallow inshore areas in the summer accounted for the higher summer incidences at Lockeport.

Annual fluctuations in incidence were great in all areas. A trend of declining incidences was noted in the southwestern Gulf of St. Lawrence where the incidence dropped from 91% in 1946 to 35% in 1956. This decline was apparently related to extensive contemporary changes in the cod fishery in the Gulf of St. Lawrence.

INTRODUCTION

Fillets of cod (*Gadus callarias*) from Canadian Atlantic waters often contain larval nematodes. All nematodes identified by us were larval *Porrocaecum*. Scott (1956) has presented evidence that all larval *Porrocaecum* in cod are *P. decipiens*. More than 50 individuals are occasionally found in fillets, and fillets with more than one or two are common. These nematodes reduce the quality of the infected fillets, and in some areas they present an important

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problem to the fishing industry. Since 1946 data on the incidence of the parasite have been collected from cod landed in Nova Scotia and New Brunswick. The present paper deals mainly with geographic and annual variations in the incidence of the parasite in cod from the southwestern part of the Gulf of St. Lawrence and along the Nova Scotian coast.

METHODS

Source of Samples

The data, except when otherwise stated, were collected by field technicians of the Biological Station, St. Andrews, N.B., at fish-packing plants at Lockeport, Lunenburg, Halifax, Canso, North Sydney and Cheticamp, Nova Scotia, and at Caraquet, New Brunswick. In these plants, cod fillets are inspected on candling tables and nematodes are picked out by an employee of the plant. One of our technicians watching this process recorded the number removed from each fillet in a sample of fillets from a known area. Each sample usually consisted of 100 fillets. When feasible, an estimate of the weight of the sample was obtained by counting the number of fillets required to fill a package of known capacity. Samples were occasionally directly examined by our technicians.

The accuracy of this method was probably not great. It depended upon the perceptiveness and diligence of the commercial picker and our observer. Since different observers often collected data at several ports from samples of the same geographic origin without appreciable differences in their results, the error attributable to their work was probably slight. Much of the inaccuracy of the commercial picker may have been caused by variations in the transparency of fillets of different sizes. A small thin fillet is translucent and nematodes are very noticeable. In contrast, a large fillet may be two inches thick and only the nematodes close to the surface would be conspicuous. The values for large fillets are probably more reduced from the actual values than are those for smaller fillets. Despite the limitations of the method in determining the exact numbers of nematodes in fillets, the relative constancy of our results for any particular geographic area indicates that the method used was sufficiently accurate for comparative purposes.

In addition to the data obtained in the above way, the incidence of infection in 61 cod from Passamaquoddy Bay, New Brunswick, was determined by the senior author.

Altogether, the incidence of the parasite was observed in about 73,000 fillets representing rather unequally about 20 fishing areas.

Treatment of the Samples

Our first step in analysis was to classify our records according to fishing areas (Fig. 1). This was usually a simple task. For example, the offshore fishing grounds of Nova Scotia consist of several well-defined banks, isolated from each other by intervening stretches of deep water. On the other hand, in most inshore areas several minor, poorly-defined localities were represented. Some arbitrary

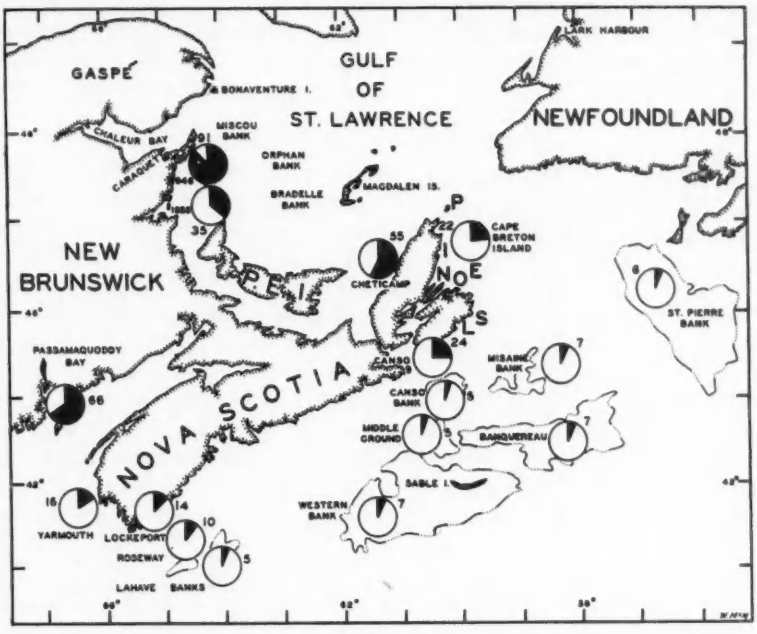

FIG. 1. Mean percentages of market cod fillets infected with larval nematodes in several east-coast fishing areas from 1946 to 1956. Cape Breton Island sampling areas were Edge of Ground (E), Ingonish (I), Louisburg (L), Inshore North Sydney (N), Offshore Sydney (O), St. Paul Island (P), and Scatari Bank (S).

definition and grouping of these localities was necessary, particularly in the Cape Breton Island area. Records from 7 localities around Cape Breton Island have been arranged in 2 groups for part of our analysis. The first, referred to as Inshore Cape Breton, includes records from cod caught near Louisburg, North Sydney, Ingonish and St. Paul Island. The second, Offshore Cape Breton, contains our records from cod caught on Scatari Bank (Fig. 1, S), about 15 miles off North Sydney (Fig. 1, O) and about 30 miles off North Sydney in a locality called Edge of Ground (Fig. 1, E). The data for the Cheticamp inshore fishery differed markedly from those for the other Cape Breton localities and have not been included in either Cape Breton group. Marked geographic changes in the distribution of the cod fishery of the southwestern Gulf of St. Lawrence have taken place since 1946 (Fig. 2). Despite some local variation in the infection within this area, the characteristics of the infections in this area appeared distinct from those of the Nova Scotian areas. Accordingly, for convenience of comparison with the Nova Scotian regions the southwestern Gulf of St. Lawrence has been arbitrarily considered as a geographic entity. Our records from the Gulf, excepting a few from the Cheticamp area, were all taken from the area bounded by Bonaventure Island, the Magdalen Islands and Prince Edward Island. This

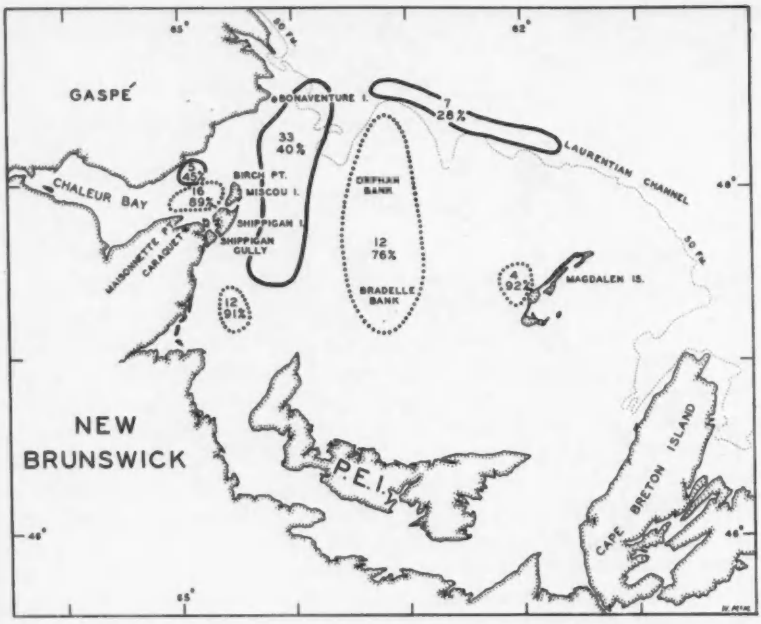

FIG. 2. Geographic source of samples of fillets of cod landed at Caraquet and examined for nematodes in 1946, 1947 and 1948 (.....) and in 1955 and 1956 (——). Numbers of samples and mean percentage of infected fillets are shown for each area.

general area has been called the Caraquet area in Table I to distinguish it from the Cheticamp area.

Cod landed at ports on the Canadian mainland are customarily divided into three size-groups: small or "scrod" (weight of single fillet under 0.4 lb.), medium or "market" (0.4 to 1.5 lb.) and large or "steak" (over 1.5 lb.). With some exceptions the samples have been grouped accordingly. Some landings, notably those from the Yarmouth and Lockeport fisheries, were sometimes not graded. In these cases since the mean weights of the samples were similar to those of market cod the mixed samples have been treated as market cod. At Caraquet, steak cod are not filleted and the remainder are not separated into market and scrod cod.

The data for scrod and steak cod were not sufficiently numerous to permit detailed analysis and only the data for market cod are considered in detail. It will be shown, however, that the conclusions derived from the analysis of the incidence in market cod are not materially altered by the data for scrod and steak cod.

Information kindly provided by Dr. W. Templeman for Newfoundland cod and by Mr. Keith Ronald for cod from the northern Gulf of St. Lawrence supple-

ments our records. The values provided by these observers were expressed as percentages of fish infected while ours were in percentages of fillets infected. This difference in expressing the incidence of infection prevented a close comparison of the two sets of observations.

GEOGRAPHIC VARIATION IN INCIDENCE

There was much geographic variation in the incidence of infection in market cod (Fig. 1 and Table I). The lowest incidences were found in cod from the offshore banks. In this region, the incidences in market cod varied from a low of 0.2% on the Grand Banks to a high of 10% on Roseway Bank. If, however, these extreme values are ignored, the incidences in cod from the remaining areas were remarkably uniform, ranging from 5% on Canso Bank, Middle Ground and Lahave Banks to 7% on Banquereau, Misaine Bank and Western Bank. The value for the Grand Banks was much lower than those for the other banks. This value, though based on only three samples, agreed closely with values based on more extensive data analyzed by Templeman (1950). In sharp contrast to the low incidences of infection in the offshore cod were the incidences recorded from the southwestern Gulf of St. Lawrence. In this region the highest incidences were observed in 1946 when the mean incidence in cod landed at Caraquet was

TABLE I. Geographic variation in the incidence of larval nematodes in fillets from three commercial size-groups of cod from Canadian Atlantic waters.

Locality	Scrod				Market				Steak			
	Number of samples	Percentage of fillets infected	Nematodes per lb. of fillet	Nematodes per fillet	Number of samples	Percentage of fillets infected	Nematodes per lb. of fillet	Nematodes per fillet	Number of samples	Percentage of fillets infected	Nematodes per lb. of fillet	Nematodes per fillet
PassamaquoddyBay	2	44	..	0.50	2	66	..	1.7	1	90	..	11.9
Yarmouth	3	7	..	0.11	18	16	0.24	0.24	5	41	..	1.0
Lockeport	32	13	0.46	0.22	72	14	0.30	0.23	13	15	0.11	0.24
Roseway Bank	3	10	0.39	0.13	8	10	0.18	0.16	..	..	..	..
Lahave Banks	8	6	0.27	0.09	41	5	0.11	0.08	9	5	0.03	0.07
Western Bank	5	7	0.13	0.07	70	7	0.09	0.08	42	8	0.05	0.12
Middle Ground	4	8	0.13	0.09	26	5	0.07	0.06	16	7	0.04	0.10
Banquereau	3	4	0.20	0.09	59	7	0.09	0.08	23	9	0.08	0.18
Misaine Bank	..	..	..	..	2	7	0.13	0.09	..	..	..	..
Canso Bank	..	..	..	..	1	5	..	0.05	..	..	..	..
St. Pierre Bank	..	..	..	..	17	6	0.08	0.06	3	3	0.02	0.03
Grand Banks	..	..	..	..	3	0.2	..	..	1	1	0.01	..
Canso	..	..	..	..	19	24	0.61	0.48	1	44	0.36	1.1
Louisburg	..	..	..	..	2	24	0.59	0.46	..	..	..	..
Scatari Bank	1	50	..	0.99	5	21	0.42	0.38	..	..	..	..
Inshore N. Sydney	..	..	..	..	9	29	0.78	0.53	..	..	..	..
Offshore N. Sydney	4	16	0.53	0.21	5	13	0.27	0.19	1	46	..	1.2
Edge of Ground	10	11	0.38	0.15	18	18	0.49	0.33	3	51	0.57	1.8
Ingonish	3	23	0.67	0.29	12	28	0.75	0.57	1	40	..	1.1
St. Paul I.	1	33	1.3	0.50	5	21	0.63	0.44	..	..	..	..
Cheticamp	1	41	2.7	0.64	3	55	2.2	1.8	2	75	2.0	3.4
Caraquet, 1946	..	..	..	..	30	91	4.2	3.8	..	..	..	..
Caraquet, 1956	..	..	..	..	23	35	0.76	0.55	..	..	..	..

91%. The mean incidence for the period from 1946 to 1956 at Caraquet was 61%. An incidence of 55% was recorded from cod caught in the Cheticamp inshore fishery. Incidences of infection in cod from inshore Nova Scotia varied widely from about 15% in western Nova Scotia to a range of 13 to 29% in the Cape Breton areas. An incidence of 66% was observed in two samples of cod caught in the vicinity of Passamaquoddy Bay.

Information supplied by Mr. Keith Ronald and Dr. W. Templeman indicated that within the Gulf of St. Lawrence the highest incidences occurred in the southwestern part. Mr. Ronald[3] observed in 1954 that about 24% of the cod along the north shore of the Gulf were infected. Dr. Templeman[3] found in 1947 that incidences varied from about 42% near Lark Harbour to about 11% farther north in the Port Saunders area in the northern Gulf. These values were appreciably lower than those recorded by us from the Caraquet and Cheticamp areas of the southwestern Gulf.

The pattern of the geographic distribution of infection described above was largely derived from our data on market cod. The values for scrod and steak cod (Table I) also illustrate the same pattern, namely, low infection in offshore fish, intermediate incidences in inshore Nova Scotian cod, and high incidences in cod from the southwestern Gulf of St. Lawrence.

A more detailed analysis of the incidence of infection in market cod from 12 areas is shown in Figure 3. As is shown in this figure the 12 areas can be separated into 4 rather distinct groups:

Western Nova Scotia—the inshore fisheries at Yarmouth and Lockeport and probably the fishery on Roseway Bank;
Offshore Banks—Lahave Banks, Western Bank, Middle Ground, Banquereau and St. Pierre Bank;
Cape Breton area—the inshore fisheries at Canso, the inshore areas of the eastern shore of Cape Breton Island, and the offshore Cape Breton fishery;
Southwestern Gulf of St. Lawrence—the Caraquet fishery.

The infection in cod in each of these groups of localities was such that the 4 groups could be clearly characterized. This is done below and in Table II.[4]

WESTERN NOVA SCOTIA. The mean incidence of infection for this area was 14%. Incidences for individual samples, however, varied between 3 and 46% with values for most samples lying between 10 and 20%. The mean number of nematodes per pound of fillet varied from 0.18 on Roseway Bank to 0.30 in the Lockeport fishery with a grand mean of 0.28 nematode for the entire group. The mean number of nematodes in each fillet was 0.23.

[3]These values were based on fish, not fillets. Our experience in the southwestern Gulf of St. Lawrence has shown, that in samples where 60 to 90% of the fish have been infected, the percentage of fillets infected has varied between 35 and 65. Accordingly, the values recorded by Ronald and Templeman should be reduced by about one third to give an approximate incidence of infection in fillets.

[4]Because of the great change since 1946 in the amount of infection in cod from the southwestern Gulf of St. Lawrence, mean values for the period 1946 to 1956 would be misleading. The 1956 values shown in Table II more accurately represent the present characteristics of the infection in the above area.

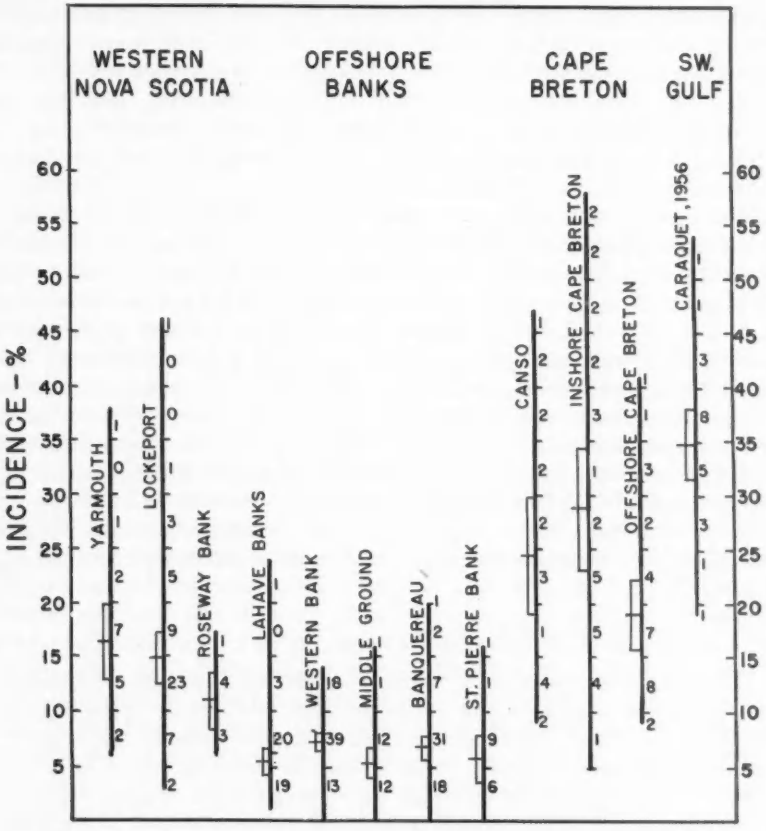

FIG. 3. Frequency distribution of percentage incidence of infection in samples of market cod fillets from 12 fishing areas from 1946 to 1956. Frequencies of samples in 5-per cent groups are indicated by the numbers to the right of each vertical bar. The small rectangles indicate the range $(M+2\sigma_M)$ to $(M-2\sigma_M)$.

TABLE II. Characteristics of nematode infections in fillets of market cod from 4 Canadian east-coast fishing areas.

	Western Nova Scotia	Offshore Banks	Cape Breton	South-western Gulf of St. Lawrence (1956)
Percentage incidence	14	6	22	35
Nematodes per pound of fillet	0.28	0.09	0.58	0.76
Nematodes per fillet	0.23	0.08	0.42	0.58

OFFSHORE BANKS. Despite the considerable distances separating the component areas of this group, the values of infection for each bank were remarkably similar. Mean incidences varied from 5 to 7% about a grand mean of 6%. Many samples were uninfected and few had incidences exceeding 15%. The mean number of nematodes per pound of fillet was low, varying around a grand mean of 0.09 from 0.07 on Middle Ground to 0.13 on Misaine Bank (2 samples only; not shown in Fig. 2). Each fillet contained on an average 0.08 nematodes.

CAPE BRETON. Incidences in samples from this area varied greatly from 5 to 58% around a mean of 22%. Most samples had incidences between 15 and 30%. However, a large proportion, almost all from the Canso and inshore Cape Breton fisheries, had incidences exceeding 40%. The mean number of nematodes per pound of fillet, 0.58, was much higher than in the two previous areas. Similarly, the average number of nematodes per fillet, 0.42, was also much higher.

SOUTHWESTERN GULF OF ST. LAWRENCE. The highest incidences of infection in the 4 groups occurred in this region. Here, in 1956, the mean incidence was 35%. Extreme values were 19 and 54%, but most samples had incidences between 30 and 40%. These values were much lower than those recorded in earlier years when, for example, in 1946 the mean incidence was 91%. In 1956 the mean number of nematodes per pound of fillet was 0.76. As in previous years, this value was clearly the highest of any area. The mean number of nematodes per fillet was 0.58.

SIZE AND INFECTION

The amount of infection, in terms of both the percentage incidence of infection and the number of nematodes per fillet, was usually greatest in steak cod and least in scrod cod (Table I). The differences between the amounts of infection in the 3 size categories varied greatly in different regions, as is shown by Table III. Here it can be seen that steak cod from the offshore banks were only slightly more heavily infected than scrod and market cod. There was no difference between the amount of infection in scrod and in market cod from the offshore banks. In western Nova Scotia there were only slight differences in infection between scrod and market cod. However, in this region the percentage incidence of infection in steak cod was distinctly higher than that in the other size-groups. Furthermore, steak cod fillets from western Nova Scotia had almost twice as many nematodes as had scrod cod. The greatest differences in infection were observed in cod from the Cape Breton fishery. In this region

TABLE III. Relation between size of cod and nematode infection in fillets of scrod (Sc), market (M), and steak (St) cod from 3 Nova Scotian fishing areas.

	Western Nova Scotia			Offshore Banks			Cape Breton		
	Sc	M	St	Sc	M	St	Sc	M	St
Number of samples	38	98	18	20	216	93	19	75	6
Percentage incidence of infection	13	14	19	6	6	8	15	22	44
Nematodes per pound of fillet	0.45	0.28	0.11	0.22	0.09	0.06	0.44	0.58	0.48
Nematodes per fillet	0.20	0.23	0.37	0.08	0.08	0.12	0.18	0.42	1.4

steak cod had an incidence of infection of 44%, a value twice as great as that for market cod and almost 3 times that for scrod cod. Steak cod fillets from Cape Breton waters averaged 1.4 nematodes per fillet, about 8 times the average number in scrod fillets.

The increase in the amount of infection was not always proportional to the increase in size. This is clearly indicated by the fact that scrod cod in samples from the offshore banks and western Nova Scotia had substantially more nematodes per pound of fillet than had market cod. The latter in turn had more nematodes per pound of fillet than steak cod. On the other hand, in the Cape Breton fishery, the increase in infection was approximately proportional to the increase in size. In this area, the number per pound of fillet was 0.44 for scrod, 0.58 for market, and 0.48 for steak cod.

Observations on the amount of infection in cod landed at Caraquet were limited principally to samples drawn from the narrow size-range of market cod. Most samples, although each was usually a mixture of scrod and market fillets, fell within the range for market fillets, that is, between 0.4 and 1.5 pounds per fillet. Scrod fillets predominated in most of the remaining samples. No samples of large steak fillets were examined. Tables IV and V present the limited data available to us.

No consistent relationship between size and infection was evident in the samples taken from Miscou Bank in 1955 and 1956. In 1955 all commercial samples averaged less than 0.6 pound per fillet. Six samples of larger fillets were specially collected from this area in 1955. Table IV shows that the infection values were not directly related to size. The heaviest infections occurred in scrod fillets and in fillets more than 1.0 pound in weight. The lightest infections were in the fillets weighing between 0.70 pound and 1.0 pound. The results of the 1956 observations disagreed with those of the preceding year. In 1956 there appeared to be a slight trend towards an increase in the amount of infection associated with an increase in the average size of the fillets.

There was an increase in the amount of infection as the size of fillets increased, in samples taken from the offshore Gulf area in the period from 1946 to 1949. The only samples of scrod had percentage incidences of 10 and 32 and had 0.27 and 0.32 nematodes per fillet. Infection values in market fillets were much higher. The minima recorded for market fillets were 61% and 1.6 per fillet. Within the market fillets, there is some evidence that the amount of infection was greatest in the largest fillets. However, since the values for individual samples within the same size-group varied greatly, this trend within the market category should be viewed with caution.

No evidence that infection increased with an increase in size of market fillets was found in inshore samples taken from Chaleur Bay in 1946 and from southeast of Shippigan Gully in the period from 1946 to 1949 (Table IV). Similar results were obtained from samples collected in 1956 from approximately the same inshore areas (Table V). This table shows that over a length-range of about 30 centimetres there was no increase with size of either the percentage incidence or the number of nematodes per fillet.

TABLE IV. The mean percentage incidence of larval nematodes and the number of nematodes per fillet in samples of successive 0.1 pound weight-groups of cod fillets collected from 4 areas in the southwestern Gulf of St. Lawrence. Numbers of samples are in parentheses.

Weight group of fillets	Miscou Bank 1955		Miscou Bank 1956		Offshore 1946–1949		SE of Shippigan Gully 1946–1949		Chaleur Bay 1946	
	Incidence	Nematodes per fillet	Incidence	Nematodes per fillet	Incidence	Nematodes per fillet	Incidence	Nematodes per fillet	Incidence	Nematodes per fillet
lb.	%		%		%		%		%	
0.30–0.39	47(3)	0.83	..	..	ca. 10[a](1)	0.27	..	..	..	..
0.40–0.49	41(6)	0.71	28(1)	0.48	32[b](1)	0.32	..	..	..	..
0.50–0.59	42(9)	0.74	35(1)	0.55	..	..	93[c](1)	4.2	..	..
0.60–0.69	..	..	35(6)	0.52	62[b](1)	1.7	87[b](1)	3.2	..	..
0.70–0.79	36(1)	0.73	36(2)	0.62	77[c,d](3)	2.1	87[d](1)	4.1	88(1)	2.5
0.80–0.89	39(1)	0.67	42(3)	0.68	84[c,d](7)	3.0	91(4)	3.3	91(4)	3.7
0.90–0.99	36(1)	0.61	42(3)	0.66	..	..	93(3)	3.2	92(5)	2.9
1.00 and up	43(3)	0.72	..	..	..	..	93(2)	4.2	93(3)	3.6

[a]Weight and incidence estimated from sample of 102 small cod (mean length 38.4 cm.) examined by senior author in 1947. Incidence originally recorded as a percentage of fish infected.
[b]Collected in 1947.
[c]Collected in 1948.
[d]Collected in 1949.

TABLE V. Percentage incidence of larval nematodes and the number per fillet in 1956 in samples, each of 300 fillets, of market cod from 3 inshore areas near Caraquet, N.B., arranged by 3-centimetre size groups.

Size-group	Maisonnette Point		10 miles N.E. of Birch Point		15 miles S.E. of Shippigan Gully	
	Incidence	No.	Incidence	No.	Incidence	No.
cm.	%		%		%	
49–51	67	1.4	0	0	100	1.0
52–54	50	1.2	50	0.67	67	1.2
55–57	55	0.83	33	0.43	58	1.1
58–60	46	0.68	52	0.77	71	1.3
61–63	53	0.83	35	0.54	58	1.0
64–66	67	1.1	45	0.70	64	1.1
67–69	60	1.2	53	0.68	58	1.1
70–72	52	0.89	33	0.58	54	1.1
73–75	50	0.67	75	1.5	81	1.3
76–78	..	..	30	0.70	38	.63
79–81	0	0	0	0	100	1.0
82–84	..	..	50	1.1	..	..
85–87	..	..	50	.75	..	..

SEASONAL VARIATION IN INCIDENCE

Only the samples from the Cape Breton fishery, exclusive of the Canso fishery, and from the Lockeport area were sufficiently extensive to permit analysis on a seasonal basis. The percentage incidence of infection in each sample of market cod from each of the aforementioned areas is shown in Figure 4. Because of rather large differences between the amounts of infection in the offshore and inshore Cape Breton areas, the incidences from these two areas have been plotted separately.

In the inshore Cape Breton area, the highest incidences were recorded in late April and May and again in late November and December. At these times almost all samples of inshore cod had incidences of 40% or more. In the intervening period usually less than 25% of the fillets were infected.

Samples from offshore Cape Breton areas showed no definite seasonal variation. However, it is suggestive that the highest incidences in this group, as for some of the inshore samples, were recorded in May.

Two samples of uncertain local origin collected near Cape Breton Island in May had more than 40% of their fillets infected, thus agreeing well with the high incidences recorded in May from inshore and offshore samples.

The highest incidences of infection in the Lockeport samples were recorded in the period from the end of April to the beginning of November. Over the entire year, most samples had less than 20% of their fillets infected. However, in the period mentioned above a relatively large proportion of the samples had incidences of infection greatly exceeding 20%. Only a single sample with an incidence of more than 20% was taken in the winter, despite the fact that most of the sampes from Lockeport were collected in the winter months.

LOCAL VARIATION IN INCIDENCE

The sampling programme in this investigation was not specifically designed to determine local variations, as distinct from wide geographic variations, in

the incidence of infection. In the course of collecting data it was, however, the impression of our field technicians that the cod caught closest to shore in the coastal waters of Nova Scotia were generally the most heavily infected. This impression was shared by fish buyers, particularly those in the Cape Breton area. The correctness of these impressions is supported by our observations in the Cape Breton and Lockeport regions (Fig. 4 and Table VI). In Table VI the samples from each area have been divided into inshore and offshore groups. Inshore samples were taken within 3 or 4 miles of shore, usually in water less than 25 fathoms deep. Offshore samples were caught at distances ranging up to 30 miles from shore in water varying in depth between 25 and 100 fathoms.

Offshore cod in the Cape Breton region were usually less frequently infected with nematodes than were the inshore cod. The mean incidence of infection was 18% in offshore cod and 27% in inshore fish.

In the Lockeport area, 34% of the fillets in the shallow-water, inshore samples were infected. The mean incidence of 13% in the deep-water samples was much lower. All the shallow-water Lockeport samples were collected in a period from April 25 to October 29. The concentration of shallow-water samples in this period acounts, at least in part, for the higher incidences observed in the Lockeport fishery during the summer months.

TABLE VI. Percentage incidence of larval nematodes in inshore and offshore samples of market cod fillets from the Cape Breton and Lockeport areas. Numbers of samples are in parentheses.

	Cape Breton	Lockeport
Inshore	27(28)	34 (6)
Offshore	18(28)	13(66)

Local variations in the amount of infection were also noted in the samples from different areas in the southwestern Gulf of St. Lawrence (Table VII). In each of the three years, 1946, 1955 and 1956, for which there were comparable samples, the offshore cod were less heavily infected than the inshore fish.

The offshore sample in 1946 had an incidence of 82% and 3.1 nematodes per fillet. These values were lower than the corresponding values in samples from 3 inshore localities. In these, the values ranged between 92 and 94% for incidence and between 3.5 and 4.0 for nematodes per fillet.

Infection values in 1955 in 2 samples from the offshore area of Miscou Bank were 40 and 42% for percentage incidence and 0.70 and 0.74 for nematodes per fillet. A sample from the inshore area of Chaleur Bay had a percentage incidence of 45% and had 0.81 nematodes per fillet.

Again in 1956 the pattern of lower infections in offshore cod was repeated. However, in 1956, the difference between offshore and inshore samples was much greater than in 1946 or 1955. Infection values for cod taken in deep water north of Orphan Bank were less than half those for cod taken southeast of Shippigan Gully.

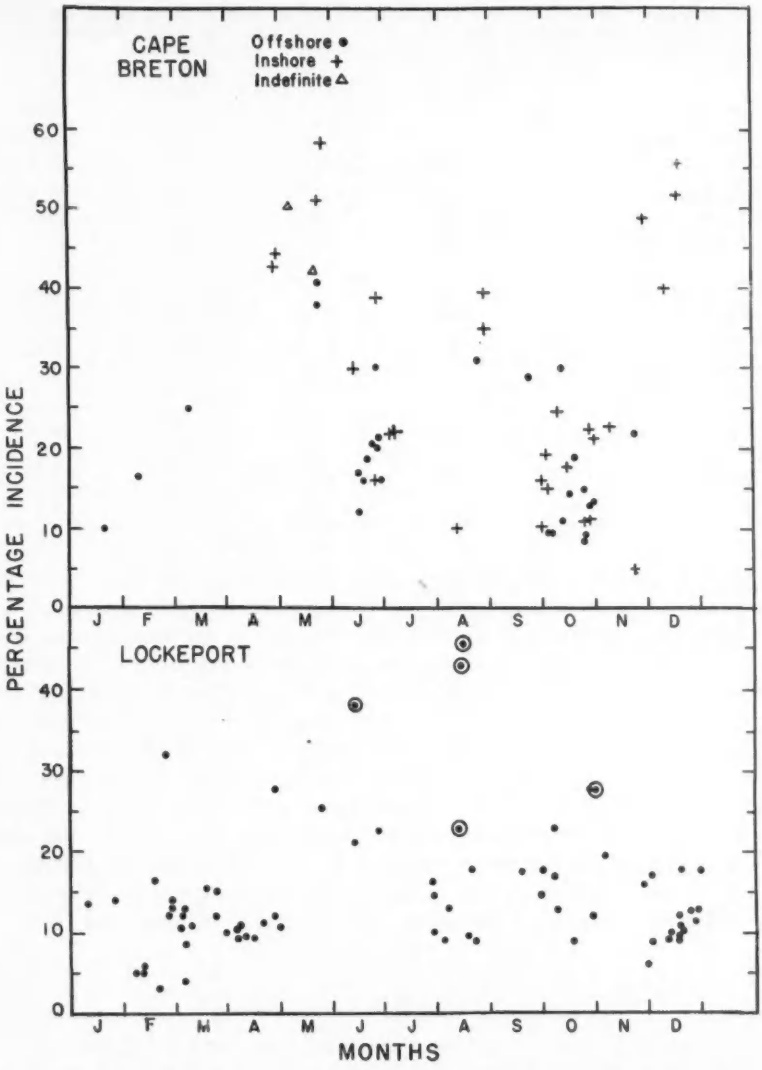

FIG. 4. Seasonal and local variation in the percentage incidence of infection in market cod fillets from the Cape Breton and Lockeport fisheries. The mean incidence of each sample is plotted. Known handline samples from shallow-water areas at Lockeport are encircled.

TABLE VII. Percentage incidence of larval nematodes, and number per fillet, in market cod from several areas in the southwestern Gulf of St. Lawrence. (The 1946 "Offshore" sample came from 3 areas: Orphan Bank, Bradelle Bank, and Miscou Bank.)

Area and year	Number of fillets	Mean weight of fillets	Nematode incidence	No. per fillet
		lb.	%	
1946				
Offshore	300	0.86	82	3.1
Inshore				
Magdalen Islands	250	0.88	92	3.7
Chaleur Bay	658	0.93	92	3.5
SE. of Shippigan Gully	500	0.95	94	4.0
1955				
Offshore				
Miscou Bank	600	0.95	40	0.70
Miscou Bank	1625	0.49	42	0.74
Inshore				
Chaleur Bay	500	0.46	45	0.81
1956				
Offshore				
Miscou Bank	1600	0.71	37	0.58
Deep water N. of Orphan Bank	700	0.72	28	0.46
Inshore				
Maisonnette Point	300	0.79	55	0.93
NE. of Birch Point	300	0.80	43	0.67
SE. of Shippigan Gully	300	0.79	62	1.1

The 1956 samples also indicated local variations within the offshore and inshore areas. In the offshore area, the infection in cod from the deep water north of Orphan Bank was appreciably less than that in cod from Miscou Bank. The highest inshore values were recorded southeast of Shippigan Gully between the New Brunswick shore and the north end of Prince Edward Island. Cod from near Maisonnette Point on the south shore of Chaleur Bay were slightly less infected than the preceding sample. The samples from Shippigan Gully and Maisonnette Point were taken by line trawl in 16 to 20 fathoms of water. The infection in the third inshore sample, taken by otter trawl in 30 fathoms of water from 10 miles northeast of Birch Point at the mouth of Chaleur Bay, was much lower than that in the other inshore samples. Indeed, the percentage incidence of 43, and 0.67 nematodes per fillet, in the Birch Point sample were only slightly higher than the values from the nearby offshore area of Miscou Bank.

ANNUAL VARIATION IN INCIDENCE

Annual variation in the incidence of infection in market cod was great in all regions. This is clearly evident in Table VIII. No consistent trend of increase or decrease in infection levels was noted in any area other than the southwestern Gulf of St. Lawrence. In this region, cod sampled at Caraquet have shown a progressive reduction in incidence from a high of 91% in 1946 to a low of 35% in 1956. Because of the sharp contrast between the situation in the southwestern Gulf of St. Lawrence and elsewhere, it seems appropriate to enquire into the reasons for this sharp decline in infection.

TABLE VIII. Annual variation from 1946 to 1956 in the percentage incidence of larval nematodes in fillets of market cod from Canadian east-coast fishing areas. Numbers of samples are in parentheses. Mean weights of fillets examined at Caraquet were of scrod size in 1952, 1953, 1955 and probably in 1954.

Area	Mean incidence 1946 to 1956	Annual mean incidence										
		1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
WESTERN NOVA SCOTIA												
Lockeport	15	13 (3)	22 (5)	12(19)	15(14)	11 (5)	16 (6)	14(11)	18 (4)	13 (5)	..	..
OFFSHORE BANKS												
Lahave Banks	6	..	10 (7)	5 (5)	5 (6)	6 (6)	4 (4)	9 (2)	3 (6)	4 (5)	..	..
Western Bank	7	..	4(9)	6(21)	8(15)	9(23)	..	8 (1)	..	5 (1)	..	..
Middle Ground	5	5 (4)	1 (6)	4 (5)	8 (9)	9 (2)	..	..	..	..	..	..
Banquereau	8	5 (2)	1 (3)	5(25)	7(18)	12 (5)	17 (1)	9 (4)	..	12 (1)	..	..
CAPE BRETON ISLAND												
Inshore (including Canso)	25	32 (6)	12 (2)	31 (6)	..	18 (4)	24 (3)	22(11)	34(12)	29 (3)	..	..
Offshore	20	19 (3)	33 (4)	26 (3)	13 (3)	13 (7)	17 (5)	19 (3)	..	..	..	..
SW. GULF OF ST. LAWRENCE												
Caraquet	61	91(30)	66 (4)	89 (4)	80 (9)	79 (1)	59 (1)	50 (7)	34 (2)	44 (5)	43(22)	35(23)

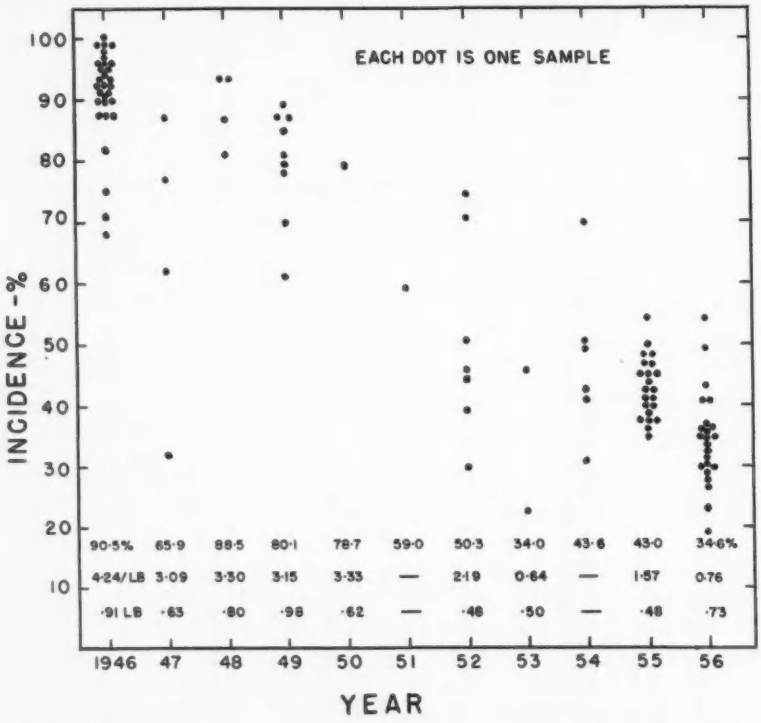

FIG 5. Percentage incidence of infection in individual samples of cod fillets landed at Caraquet from 1946 to 1956. For each year, the mean percentage incidence, the mean number of nematodes per pound of fillet, and the mean weight of each fillet are also shown.

Figure 5 shows that the incidence of infection in cod landed at Caraquet has decreased from a range of 68 to 100% in 1946 to a range of 19 to 54% in 1956. Meanwhile the number of nematodes per pound of fillet dropped from 4.24 to 0.76. Although there is less information on incidence in most of the intervening years, it is sufficient to show that the values in 1946 and 1956 were not exceptional. The data further indicate that the greatest drop in incidence occurred between 1949 and 1952. The incidences in samples taken before 1950 were mostly above 80%, after 1951 mostly below 50%. Figure 5 also shows that the decrease in incidence was accompanied until 1956 by an appreciable decrease in the average weight of the fillets examined. This decrease in weight, like that in incidence, was most marked in the years following 1949. In 1956, the average weight of fillets increased greatly, but the incidence of nematodes continued to decline.

Only 2 samples of cod fillets of weights less than 0.5 pound per fillet from the southwestern Gulf of St. Lawrence were examined by us in the period from 1946 to 1949. These samples, referred to earlier in Table IV, had incidences of

infection of 10 and 32%. These incidences are less than those in scrod cod at the present time. Accordingly, it appears that there has been no decrease in the incidence of infection in scrod cod in the Caraquet area since 1946.

In contrast to the absence of a decrease in the incidence of infection in scrod cod, there has been a marked reduction in the number of nematodes in market cod. This is obvious from a comparison of the infection values in fillets of similar weights in 1946, 1955 and 1956 (Table VII). In 1946, the incidence of infection was 82% in the offshore sample. In 1955 and 1956, respectively, the incidences in offshore samples were 40% and 37%. Similar large reductions in the amount of infection were noted in inshore market cod. In these fish, the incidence declined from more than 90% in 1946 to incidences ranging from 43 to 62% in 1956.

The decline in the number of nematodes in market cod in the last decade occurred in all areas in the southwestern Gulf of St. Lawrence for which there were comparable records (Table VII). There are insufficient data to show whether the decrease in infection was more marked in one area than in another.

The decrease in the amount of infection in commercial cod from Gulf areas coincided with extensive changes in the cod fishery. The only explanations of the reduction in infection that can be suggested with our present knowledge are related to these changes.

During the period from 1947 to 1954 the Caraquet fishery changed almost completely from line fishing to dragging. Coincident with this change there was the increased use of offshore areas which was noted earlier (Fig. 2). There have also been significant changes in the age composition of landed cod since 1948 (Fig. 6). In this year and in the two subsequent years more than half the landed cod were older than 7 years. In the early catches, cod 10 years old or more formed an important part of the catch. Subsequently, younger age-groups dominated the catches. In 1952, 1955 and 1956, most of the landed cod were less than 8 years old. In 1955 and 1956, cod of 10 years or older were relatively much rarer than they were in the earlier years. The growth rate of cod in the Caraquet area has increased in recent years, most noticeably in the older age-groups. Figure 7 shows that on the average the age of a market cod, 70 centimetres long, in 1956, was about 7 years. In 1948 the age of cod of the same length averaged about 9 years.

Some of the reduction in the infection in cod may be attributed to the shift from a predominantly inshore fishery to an offshore fishery. Since offshore samples have generally been less heavily infected than inshore samples, catches in recent years, consisting as they have mostly of offshore fish, would have a lower incidence. However, this explanation can at best account for only a part of the reduction since inshore as well as offshore samples have shown substantial reductions in the amount of infection. Most of the decline in incidence is more likely related to other changes in the fishery.

Part of the reduction in the number of nematodes may be attributed to the recent occurrence of younger cod in the landings at Caraquet. There has apparently been no appreciable change in the incidence of infection in young cod since 1947 as far as can be determined from only 2 samples of young cod taken

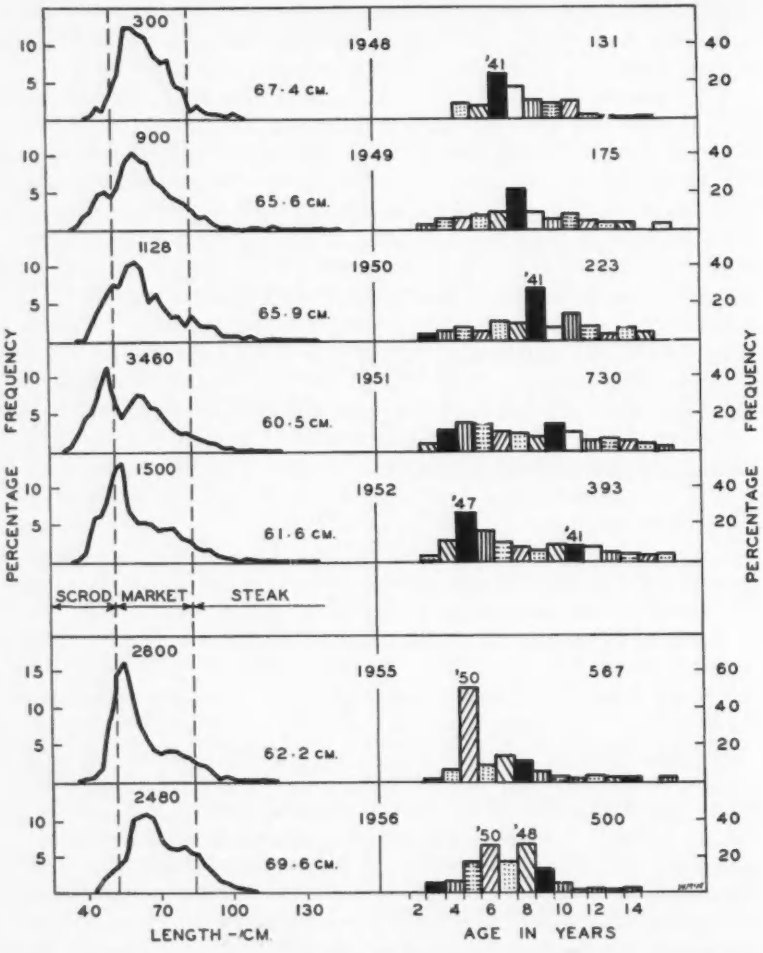

FIG. 6. Annual variation in size and age composition of Caraquet cod landed in the months of August to October, 1948 to 1956. Numbers of fish sampled and mean lengths in centimetres are noted.

in 1947 (Table IV). If this is true, then the large number of young cod now found in commercial landings would result in a reduced incidence of infection in commercial samples. This explanation, however, does not account for the reduction in incidence observed in large market cod.

The decline in incidence in market cod may be attributed to the lower average age of this size-group of cod. The difference in the age of comparable sizes of large market cod landed in 1948 and 1956 amounted to at least 2 years.

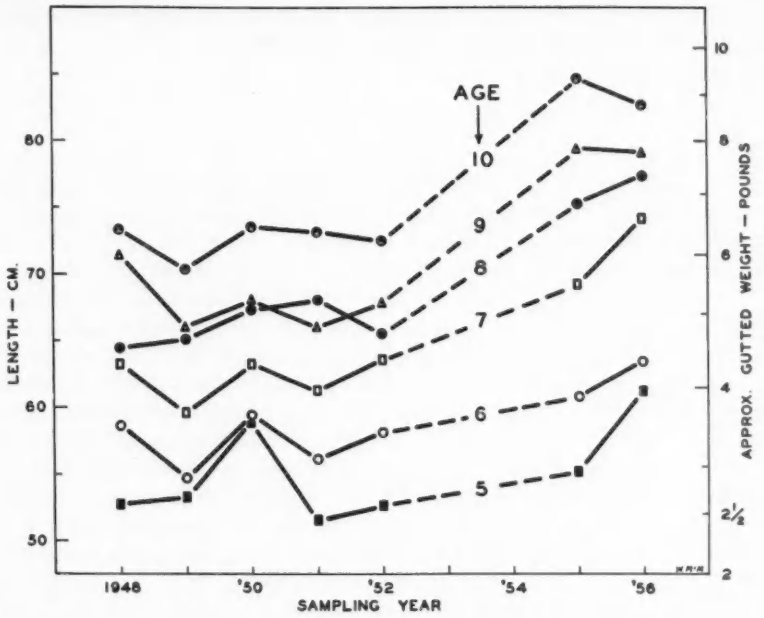

FIG. 7. Annual variation in growth of Caraquet cod landed in the months of August to October, 1948 to 1956.

Accordingly, large market cod in 1956, being younger than cod of a similar size in 1948, would have had less opportunity to become infected.

The principal weakness of our argument about market cod is that we have been unable to demonstrate any marked increase in incidence with increasing size, and presumably age, in the market cod category. However, in other regions larger cod had more nematodes than smaller. Furthermore, Ronald (personal communication) and Marcotte (1952) found in the southwestern Gulf of St. Lawrence that there was a gradual increase in infection with size. Until the inconsistencies of the data bearing on the relation between age and infection can be resolved, the suggested explanation accounting for the reduction of incidence in market cod must be regarded as conjectural.

We have assumed that the reduction in incidence has been related only to changes in the dynamics of the cod populations in the southwestern Gulf of St. Lawrence. This has been done simply because there was no reasonable alternative. There is an almost complete lack of information on the effect of other animals or hydrographic factors upon the abundance of the parasites. It is known, however, that the abundance of seals, the definitive hosts of the nematodes, has not changed materially since 1946 (H. D. Fisher, personal communication). McLellan and Lauzier (1955) have shown that annual mean water temperatures in the southwestern Gulf of St. Lawrence have fluctuated widely since 1945.

There is nothing in their records to suggest that the irregular changes in water temperatures are importantly related to the decline in the abundance of nematodes in cod.

DISCUSSION

The present study has shown that the infection of cod fillets with larval *P. decipiens* varied in a consistent geographic pattern. The fact that this pattern of geographic variation has remained unchanged over a 10-year period is conclusive evidence that discrete populations of cod are present in east-coast waters.

The above conclusion agrees with the observations of McKenzie and Smith (1955). They demonstrated that there are several distinct inshore and offshore populations of cod along the Nova Scotian coast as well as several populations in the southwestern Gulf of St. Lawrence. Our observations support their contention that there is little mixing of inshore and offshore populations. In this connection it is noteworthy that the incidence of infection in market cod from Canso Bank agreed with those from the other offshore banks rather than with the high incidence characteristic of the nearby inshore fishery at Canso. That some mixing of populations does occur is indicated by the records for Roseway Bank which is intermediate both in position and infection values between the inshore Lockeport area and the offshore Lahave Banks. McKenzie (1934, 1956) and McCracken (1956) have shown that there is some movement of cod between the inshore area and Roseway Bank but little beyond to the Lahave Banks. The extreme variability of the samples in the Cape Breton area can be attributed to seasonal changes in the distribution of cod populations around Cape Breton Island. McKenzie (1934, 1956) and F. D. McCracken (unpublished MS.) have established that there are extensive seasonal movements of cod between the offshore banks, the Cape Breton area and the southwestern Gulf of St. Lawrence. The lower incidences of infection in cod from the Cape Breton area in the summer can be interpreted in the light of these seasonal movements of cod. Some cod from the heavily-infected Caraquet area move south in the late fall to the Cape Breton area and return to the area around Caraquet in the spring. Cod from the lightly-infected offshore banks tend to move to the Cape Breton area in the late spring and return offshore in the fall. These seasonal migrations apparently result in lowered incidences of infection in cod around Cape Breton in the summer.

The geographic distribution of infected cod is related to the distribution of seals in which larval *P. decipiens* mature and reproduce. According to Fisher (1950), one species, the harbour seal (*Phoca vitulina*), is common and widely distributed along the east coast of the southern Canadian mainland. Another species, the gray seal (*Halichoerus grypus*), is less common and less widespread than the harbour seal. Both are common hosts for *P. decipiens* (Scott and Fisher, MS). A third species, the harp seal (*Phoca groenlandica*) is very abundant in the winter and in the spring in the Gulf of St. Lawrence. Seals are the only known definitive hosts in Canadian waters of *P. decipiens*. Accordingly, the restriction of seals to inshore waters and to the Gulf of St. Lawrence would tend to bring

the larval nematodes into contact with cod in those areas. Conversely, the scarcity of seals in offshore waters would greatly reduce the chances of offshore cod becoming infected. Colonies of harbour and gray seals do occur away from the mainland on Sable Island and Miquelon Island. These offshore seals may contribute to the infection in offshore cod. Harbour and gray seals are the only common seals in the Bay of Fundy, along western Nova Scotia, and near the offshore banks. We conclude therefore that in these regions the infection in cod must be derived from harbour and gray seals. Elsewhere, around Cape Breton Island and in the Gulf of St. Lawrence, the situation is complicated by the presence of the migratory harp seal as well as the other two seals. The harp seal, when present in the Gulf of St. Lawrence, is much more numerous than the combined populations of harbour and gray seals. Thus, the harp seal probably accounts for the higher incidence of infection in cod from the Cape Breton region and the southwestern Gulf of St. Lawrence. However, the significance of marked seasonal variations in the incidence of *P. decipiens* in the harp seal is not yet understood. Consequently, we cannot say categorically why the cod of the southwestern Gulf of St. Lawrence and the Cape Breton area should be more heavily infected than elsewhere.

The fact that steak cod usually had more nematodes than smaller cod is evidence that cod are subject to successive infections throughout life. In most regions, however, the infection did not greatly increase after scrod size had been reached. Therefore, the opportunities to become infected cannot be equally numerous at all stages in the life of cod. Rather they must be most numerous when cod are small. It would thus seem that there is some aspect of the life of young cod which exposes them to infection more frequently than large cod. Unfortunately, the life-history of the parasite (Scott, 1950) between the time when the parasite leaves the seal as an egg and the time when it appears in fish muscle as a large larva is almost totally unknown. Consequently, we can only suggest that the changes in feeding habits which undoubtedly accompany changes in the size of cod may influence the rate of infection in different sizes of cod.

The incidence of infection in commercial landings may be influenced by the stability of the fishery in the area concerned. A decline in the incidence of infection in the southwestern Gulf of St. Lawrence has been related to contemporary extensive changes in the cod fishery in that area. On the other hand, in Lockeport area where the cod fishery has been relatively stable there has been no apparent continuing change in the incidence of infection.

ACKNOWLEDGMENTS

We wish to thank Mr. Keith Ronald, Department of Fisheries, Quebec, and Dr. W. Templeman, Fisheries Research Board of Canada, St. John's, Newfoundland, for permission to use some data from their unpublished studies on the incidence of nematodes in cod. Most of the data in this paper were collected by Mr. D. N. Fitzgerald. His contribution is gratefully acknowledged. We acknowledge also the assistance of several technicians, especially that of Mr. A. C. Kohler, who were responsible for the age determinations of cod.

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CORRECTIONS FOR RECENT PUBLICATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA

Bulletins of the Fisheries Research Board of Canada

No. 107—"THE FIRST TEN YEARS OF COMMERCIAL FISHING ON GREAT SLAVE LAKE," by W. A. Kennedy.

Page 49, item 4, line 2: The figure 0.05 should read 0.005.

Journal of the Fisheries Research Board of Canada

VOLUME 11, No. 5—paper by R. E. S. Homans and V. D. Vladykov: "RELATION BETWEEN FEEDING AND THE SEXUAL CYCLE OF THE HADDOCK."

Page 538: Line 11 from the bottom should be transposed to the bottom of the page.

VOLUME 12, No. 5—paper by A. L. Tester: "ESTIMATION OF RECRUITMENT AND NATURAL MORTALITY RATE FROM AGE-COMPOSITION AND CATCH DATA IN BRITISH COLUMBIA HERRING POPULATIONS."

Page 651, footnote: the last formula (not numbered) should read:

$$R = \frac{e^{t_1 - t_2} C_1 a_1 - C_2 a_2}{e^{t_1 - t_2} - 1}$$

VOLUME 12, No. 5—paper by G. R. Vavasour and A. A. Blair: "POLLUTION SURVEY OF HUMBER ARM AND EXPLOITS RIVER."

Page 685, Table I, Station III: The depth immediately below 10 metres should be 20 instead of 10.

Page 692, Table IV, Station IV: The depth should be 1.5 instead of 5.1.

VOLUME 14, No. 1—paper by J. R. Vallentyne: "THE MOLECULAR NATURE OF ORGANIC MATTER IN LAKES AND OCEANS, WITH LESSER REFERENCE TO SEWAGE AND TERRESTRIAL SOILS."

Page 82, paragraph 3 of Addendum, line 2: Instead of *p*-hydroxybenzene, read *p*-hydroxybenzaldehyde.

VOLUME 14, No. 3—paper by J. P. Tully and Allan J. Dodimead: "PROPERTIES OF THE WATER IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA, AND INFLUENCING FACTORS."

Page 298: the parenthesized formula for bicarbonate ion in the last line of text should read as in the first equation below that line.

VOLUME 14, No. 3—paper by Michael Waldichuk: "PHYSICAL OCEANOGRAPHY OF THE STRAIT OF GEORGIA."

Page 459, first line of text below equation (31): S^0 should read S_0. In the next line, t should read $t_{\frac{1}{2}}$. In the first line of text below equation (32), t should read $t_{\frac{1}{2}}$.

VOLUME 14, No. 4—paper by C. H. Castell and Maxine F. Greenough: "THE ACTION OF *Pseudomonas* ON FISH MUSCLE: 1. ORGANISMS RESPONSIBLE FOR ODOURS PRODUCED DURING INCIPIENT SPOILAGE OF CHILLED FISH MUSCLE."

Page 618: The last two lines should be transposed.

Page 625: The date of the Shewan (*et al.*) reference should read 1953 instead of 1935.

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